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MARINE PHYTOGEOGRAPHY

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From a comparative study of marine floras we may at some date be able to demonstrate the evolution of sea plants in both time and space. At present it is impossible to complete this comparative study since the algal exploration of many parts of the world is incomplete. Further, algal taxonomy lags far behind the corresponding study of land plants. Thus any theory of phytogeography based on our present knowledge of marine plants rests on an insecure foundation.

Variation in algal communities, within small areas, can be explained satisfactorily in terms of changes in exposure to dessication or heavy seas, changes in mineral and gaseous supplies, in intensity of light and heat, depth of water, and the nature of the sea floor. On this there are superimposed seasonal changes in the flora and interaction or competition between organisms.

When a comparison is made of more widely separated districts, however, such explanations are inadequate. The original conception of algal distribution was that each species had a centre of growth from which it was disseminated following the lines of the coast, each species being influenced by local factors such as depth of water. This idea accounted for local richness in certain groups of the flora and also the similarity between the algal floras bordering an ocean. Exceptions were quickly noted, however, many plants (e.g. *Codium tomentosum*) being reported as cosmopolitan in distribution. Later work, as explained below, has suggested that this supposed cosmopolitan distribution may, in at least some cases, be due to taxonomic errors.

By 1849 we find Harvey coming to the conclusion that temperature zones were highly important. Thus, in number of species, the "browns" (Melanophyceae) predominated in the tropics, the "reds" (Rhodophyceae) reached a maximum in the temperate zones, and the "greens" (Chlorophyceae) were polar or universal.

Zoning by temperature may well be a misnomer for zoning by light intensity, as has been emphasized by Tilden.

Besides this zoning by latitude, a certain amount of data indicates zoning by longitude; for instance in the Codiaceae, A. & E. S. Gepp (1911) state that five large genera are widely distributed in both hemispheres,

seven genera are in the Eastern Hemisphere only, one in the West Indies region and one in the Mediterranean Sea. Only very few species occur in both hemispheres. This grouping would seem due to some barrier (past or present) preventing east-west migration.

Discontinuity of distribution has been attributed to the presence, or past existence, of barriers such as land masses, ocean deeps, or sandbank deserts. Likewise, wide dispersal has been explained as due to distribution by birds, ships, etc., and by ocean currents (speed as well as direction being important because the time of life of motile spores is limited). Svedelius (1924) suggested that the present distribution of algae may be due to geological changes in land and sea allowing migration by way of water connections from the Indian Ocean to the Mediterranean Sea via Suez, and from the Pacific to the Atlantic Ocean via Panama. Our present knowledge is too meagre to test this theory.

Fossil evidence is unsatisfactory because algal forms are usually soft, and hence their remains are scarce except for the specialized calcareous seaweeds of many so-called "coral" reefs. Lucas (1927) reported the discovery of *Bytholotrephis gracilis* James & Hall, from Victoria, Australia, "apparently identical" with forms found in the Lower Ordovician beds of North America. Another fossil species was like one found in England. Lucas assumed that *Bytholotrephis* was an "elemental or generalised type," dominant in England, North America, Australia, etc. This idea of an elemental or generalized type represents a theory that at one time uniform conditions and marine floras existed throughout the world. Later more temperate conditions prevailed north and south of the tropics and the floras of these zones, subjected to similar environments, changed along similar lines. Finally, it was suggested that, in the frigid zones, we would have identical representatives which were absent from temperate or torrid zones. This argument may hold for plankton (which are not considered in this article) but Gain (1912) has shown that great differences exist between the marine floras of the Arctic and Antarctic. For instance, he noted that not one species of the large groups of Fucaceae and Laminariaceae was common to both zones, although all species of these groups belong to cool regions.

May (1940) applied Jaccard's Coefficient of Correlation to the marine floras (Chlorophyceae and Melanophyceae only) of Australia, New Zealand, Britain, and North America; also of Australia-Cape of Good Hope. From figures published by Gain (reference given above) the coefficient percentages for the Arctic and Antarctic floras are:

Chlorophyceae 10.5 Melanophyceae 6.9 Rhodophyceae 7.8

All these coefficients are surprisingly alike and show that the degree of uniformity of the floras of the places examined is fairly constant. The correlation tends to be higher among the Chlorophyceae than the Melanophyceae. The Chlorophyceae include more so-called "cosmopolitan" species.

It seems the wide distributions reported for so-called "cosmopolitan" plants may very well be due to faulty systematic work. Setchell (1914) examined *Scinaia furcellata*, previously reported as "cosmopolitan." He found that this species was in reality limited in distribution. Plants reported under this specific name as occurring in other districts were either different species or even different genera. Thus the "cosmopolitan" distribution resolved itself into there being a group of more or less closely related species, each occupying its own limited region.

Ectocarpus confervoides, on the other hand, appears to be truly cosmopolitan, but different phases of its life history predominate in different places. The reason for this is not understood, although the appearance of many algae is known to change with habitat, i. e. the form assumed depends on the environment.

Weber van Bosse (1904) reported that many characters used in classifying plants "were not implicitly to be relied upon in all species." These characters included manner of ramification, diameter of conceptacles, and the number or manner in which they appear on the joints, characters which are still widely used. Perhaps the present unsatisfactory condition of algal systematics could best be overcome by more care being paid to the criteria used in classification. Certainly we need more knowledge of the specific limits of the plants we deal with before a phytogeographic comparison between floras can be satisfactory.

To conclude, phytogeography of marine plants is an almost untouched field. Without more work of systematic nature and further collections being made, this study is unable to advance beyond vague hypotheses. All we can say with certainty is that latitude and the presence or absence of barriers (either geological or present-day) between suitable habitats appear to control the distribution of marine vegetation.

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GALAXAURA, A DIPLOBIONTIC FLORIDEAN GENUS WITHIN THE ORDER NEMALIONALES

NILS SVEDELIUS

One of the most remarkable discoveries in the sphere of floridean researches was the observation of M. A. Howe (1917, 1918) that in the genus *Galaxaura* there is a structural dimorphism of sexual and tetrasporic plants. This was previously quite unknown in this algal group and the discovery was the more remarkable since this genus belongs to the order *Nemalionales* among the Florideae, which order comprehends especially haplobiontic types, i. e., such types in which the reduction division occurs immediately after the fertilization of the female nucleus and in which there is therefore no tetraspore formation whatsoever. This structural dimorphism in respect to the anatomy was naturally quite unknown to F. R. Kjellman when, in the year 1900, he published his comprehensive treatise of the genus *Galaxaura* and to a great extent based the diagnoses of the sections in particular on anatomical characters. These sections of Kjellman contain either purely sexual or purely tetrasporic plants. After Howe's discovery, this classification was quite untenable and it is now an important task for algological research to unite Kjellman's different species which are, as we now know, only different generations of one and the same species. The consequence of all this is that a close investigation of the development of *Galaxaura* is highly necessary, the more so as the divergent anatomy of the sexual and the tetrasporic plants also must be made clear from the developmental point of view.

I have delivered a contribution to the solution of these problems in a paper "Zytologisch-entwicklungsgeschichtliche Studien über Galaxaura, eine diplobiontische Nemalionales-Gattung" (1942) and I will here give a short account of its main results. This seems to be all the more required as *Galaxaura* in many other respects too proved to be a new and rather divergent type of organization amongst the Florideae.

By my investigations, I believe I have established that the sexual and the tetrasporic plants are also distinguished by a certain difference regarding their ramification and succession of shoots. The sexual plants have a more lively ramification caused by proliferations from new growing points, whereas the tetrasporic plants have poorer, mainly dichotomous ramification and a more continuous apical growth. This seems to depend upon the fact that the fertile shoots of the sexual plants are commonly almost totally thrown off after fertilization, whereas the tetrasporic shoots are not deformed to such a high degree by the formation of tetraspores, but can survive and continue their growth.

The dimorphism regarding the anatomy that Howe first observed is restricted to the assimilating layer of the cortex, and depends on a very early differentiation, just below the growing point, which appears in such a way that the cortex of the tetrasporic plants produce still another cell-layer besides those belonging to the sexual plants. The assimilating cells

of the tetrasporic plants are supported by special stalk-cells and the cells lying between these stalk cells develop in another way. Either they become stretched laterally with the result that the assimilating cells are isolated from each other so that small cavities are formed between them, or else they develop into big, rounded, colorless cells between the stalk-cells.

Earlier statements about the cystocarp of *Galaxaura* are very scarce and, moreover, quite false. Thus the statement that the cystocarp of *Galaxaura* has an involucre or pericarp formed from the lowest cell of the carpogonial branch is incorrect and derived from a false observation. In this, *Galaxaura* differs from both *Scinaia* and *Gloiophloea, Pseudoscinaia* and *Actinotrichia.* On the other hand, *Galaxaura* in this respect agrees with *Chaetangium* (Martin 1939).

The side branchlets of the three-celled carpogonial branch develop very early and become large, and rich in plasmatic content, but with very weakly staining nuclei. Further, *all the cells of side branchlets get fertilized diploid nuclei.* After fertilization, the diploid nucleus either enters directly into the hypogynous cell (*G. corymbifera*) or first divides once in the carpogone itself, after which the daughter nuclei migrate into the different inferior cells (*G. Diesingiana*). In the emigration of the fertilized nucleus from the carpogone, *Galaxaura* corresponds with *Scinaia* and *Chaetangium,* but differs from these genera in an important respect: *no immediate reduction division occurs in Galaxaura,* which thus is a diplobiontic genus within the *Nemalionales* having special diploid tetrasporic plants with the reduction division at tetraspore formation. This I have plainly observed in *G. Diesingiana* and *G. tenera.*

When the diploid nuclei have entered the hypogynous cell, a lively nuclear division arises, and these diploid nuclei enter all the cells of the branchlets of the carpogonial branch except the empty carpogonium itself. Open pore connections now arise between the hypogynous cell and the cells of the side branchlets. The gonimoblast filaments soon begin to develop and elongate in different directions, namely: 1) straight upwards, i. e., through the basal part of the carpogonium; 2) laterally from the side branchlets of the hypogynous cell; 3) from the first or lowest cell of the carpogonial branch. It ought to be pointed out that there is a differentiation between such gonimoblast filaments as grow straight upwards and begin the carpospore formation immediately, and those that later on grow out laterally, giving rise to *secondary* gonimoblast centra. Finally, there are also formed sterile nutritive filaments which grow downward and seek out the bigger leading cells in the center of the alga, which cells become twined round by these nutritive filaments. All gonimoblasts, the primary as well as the secondary, have, however, a common ostiole through the calcified cortical layer. The unity of the cystocarp is maintained in spite of several distinct gonimoblast centers.

Regarding the formation of the carpospores, it is to be observed that, after they have been dispersed, regeneration generally takes place so that

new sporangia are formed underneath the emptied ones. On the other hand, no paraphyses are formed, just as in *Scinaia*. Statements about paraphyses in *Galaxaura* in the literature are false, as are the statements about a special pericarp formed by filaments from lower cells of the carpogonial branch.

Thus the formation of the cystocarp in *Galaxaura* has been found to be a type which is quite new among the Rhodophyceae, and characterized by the fact that *the whole carpogonial branch receives diploid nuclei*, and that the whole carpogonial branch also forms starting-points for the gonimoblast. *The carpogonial branch can be comprehended as a compound auxiliary system.* The whole gonimoblast can be divided into primary and secondary gonimoblasts whereby the primary is the one which is formed in connection with the central fusion-cell, and the secondary the one originating from the centers which have proceeded from the horizontally extending gonimoblast filaments.

Galaxaura is also remarkable for the fact that its spermatangia are formed in deep cavities, a very exceptional case among the Rhodophyceae. An investigation of the development has proved, however, that the very earliest stages correspond rather well with those of *Scinaia*, but in *Scinaia* the spermatangial branches protrude and push between the epidermal cells to become superficial. In *Galaxaura* the development proceeds in another direction. The branching is especially lateral, and the surrounding cortex cells stretch around the spermatangial branchlets with the result that they very early become depressed in a deep cavity, the walls of which are covered by the spermatangial branchlets. However different the spermatangial branches in *Scinaia* and *Galaxaura* may still seem in fully developed stages, when the development has been clarified, they can without difficulty be classed under a uniform scheme or type of organization.

The genus *Galaxaura* belongs among the very few genera amongst the *Nemalionales* which are characterized by the formation of tetraspores. As it has now been proved that *Galaxaura* is a real diplobiont, there is of course no reason to suppose anything else than that the tetraspore formation is also combined with a reduction division. I have also been able to prove this reduction division in two species belonging to two different sections, namely *G. Diesingiana* and *G. tenera*. It proceeds normally and the nucleus of the tetraspore mother-cell passes through prophase with spireme and diakinesis with about ten bivalents (gemini).

The position of the tetrasporangia varies in different species and on this a division of the genus *Galaxaura* into sections may be founded better than on the older one which was based mainly upon anatomical characters. Preliminarily, I divide *Galaxaura* into three sections, namely:

Sect. 1. *Rhodura* (Kjellm.) Sved. emend., characterized by quite sessile sporangia formed terminally or laterally upon rather long assimilation filaments. The sporangia never regenerate.

Sect. 2. *Acrosporangiatae* Sved., characterized by terminal sporangia formed upon assimilating cells from a special small stalk-cell. After the dispersion of the tetraspores, the stalk-cell forms a new tetrasporangium in which the nucleus passes through a new reduction division and a new tetrad is formed. This process is repeated many (5–6) times, and after each regeneration the basal part of the regenerated sporangium always remains as a collar at the base of the new sporangium. Sometimes a new and purely vegetative cell is interpolated between the sporangia.

Sect. 3. *Pleurosporangiatae* Sved., characterized by the constantly lateral sporangia originating from the assimilating cells by means of a special stalk cell. Regeneration occurs here also but, in contrast to the section *Acrosporangiatae*, only once.

The repeated regenerations combined with *repeated* reduction divisions is very remarkable and with no equivalent in any other floridean genus.

An investigation of the closely related chaetangiaceous genera *Scinaia, Chaetangium,* and *Galaxaura* has shown that the first two genera are haplobiontic and lack tetraspore generation, whereas *Galaxaura* is diplobiontic with special tetrasporic plants. According to statements in the literature, *Gloiophloea* and *Pseudoscinaia* are very probably haplobionts, whereas, as I have now shown, *Galaxaura* is diplobiontic with special tetrasporic plants. *Actinotrichia* is also diplobiontic. Thus it is evident, just as I have already pointed out in my *Scinaia* paper of 1915, that we must be very careful to use haplo- and diplobiontic organization as a systematic character for characterizing the larger groups. Closely related genera behave differently in this respect and in the genus *Chantransia* even different species behave differently. Thus it is impossible to make haplobiontic organization into a main character for the order *Nemalionales* even if the majority of its genera are haplobionts. It seems to me that this character must not be accorded higher taxonomic value than, for example, homospory and heterospory for the taxonomy of the Pteridophyta. We may say that in the order *Nemalionales* we find amongst the Rhodophyceae the transition types between haplobiontic and diplobiontic organization, that is, the organization which later becomes the predominant one of the higher Red Algae.

Regarding the special taxonomy of the family *Chaetangiaceae* I here give a revised classification in which the two subfamilies *Scinaiae* and *Chaetangieae* are maintained with partly altered diagnoses:

Subfamily I. *Scinaieae* (Trevis.) Sved. emend.

The lowest cell of the carpogonial branch forms a sterile pericarp around the gonimoblast, i. e. the cystocarp is provided with a wall. The spermatangia are generally superficial.

A. Haplobionts: *Scinaia, Gloiophloea, Pseudoscinaia.*

B. Diplobiont: *Actinotrichia.*

Subfamily II. *Chaetangieae* (Kuetz.) Sved. emend.

The sterile pericarp about the gonimoblast lacking; gonimoblast developing from nearly all cells of the carpogonial branch, the cystocarp is thus without wall. Spermatangia are immersed in cavities.

A. Haplobiont: *Chaetangium.*

B. Diplobiont: *Galaxaura.*

It appears from this system that *diplobiontic organization must have*

arisen at different occasions during the evolution of the Chaetangiaceae. This seems to me to be of great interest and it is also of fundamental importance for the real understanding of the evolution of the plants from haploid to the prevailing diploid organization.

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MORPHOLOGIC AND PHYSIOLOGIC INVESTIGATIONS IN DIATOMS

Sten Wiedling

Having earlier studied culture methods for planktonic fresh-water algae, especially diatoms, the author in 1934 started an experimental investigation of the Nitzschiae with the intention of finding out the conditions of auxospore formation in these diatoms. Both fresh-water forms and those from brackish and salt water were cultured (Botaniska Notiser **1941:** 37. 1941). The list of species according to the determinations of Dr. Astrid Cleve-Euler, the grand old lady of Scandinavian diatomology, comprises the following forms: *Nitzschia ovalis* Arnott fa., *N. subtilis* var. *paleacea* Grun., *N. palea* var. *debilis* (Kg.) Grun., *N. palea* var. *tropica?* Grun., *N. Kützingiana* Hilse, *N. Kützingiana* var. *exilis* Grun., and *N. communis* Rabenhorst.

In all, about twenty-five strains were kept and some of them are still being cultured. Three standard substrates were used, all of them based on agar and inorganic salts; ferric citrate, however, was added as an iron source since Carsten Olsen in 1929 demonstrated its superiority to inorganic iron salts in plant cultures. For the fresh-water forms, distilled or tap water was added and for the other forms surface water from the Sound was found suitable (cf. Harvey, J., Marine Biol. Assoc. **23:** 499. 1939).

The results of this investigation on the reproduction of the Nitzschiae were partly not according to expectation (Naturwiss. **31:** 115. 1943). Several strains as those of *N. subtilis* var. *paleacea* Grun., *N. Kützingiana* Hilse, and *N. palea* var. *debilis* (Kg.) Grun. did not show any decrease in the apical length, which instead was constant. This experience is another evidence against the universal significance of the MacDonald-Pfitzer rule for diatom variation (J. D. MacDonald, Ann. Mag. Nat. Hist. **3:** 1. 1869; E. Pfitzer, Sitzungsber. Niederrhein. Ges. Natur-Heilkde, Bonn **1869:** 71; Bot. Zeitung **27:** 779. 1869). Other diatoms with constant apical length were earlier found by Allen and Nelson (*N. closterium* W. Sm. fa. *minutissima*, Journ. Mar. Biol. Assoc. **8:** 421. 1910) and Geitler (*Eunotia pectinalis* var. *minor* (Kütz.) Rabenh., Arch. Protistenk. **78:** 1. 1932). The forms with a constant apical length may represent a certain stage in the phylogenetic development of diatoms. Evidently our views on diatom variability and reproduction must be thoroughly revised.

Another interesting item was the formation of cell aggregates ("colonies") of a typical appearance ("forma multiplex") in the otherwise solitary *N. Kützingiana* var. *exilis* Grun. (Botaniska Notiser **1940:** 403. 1940). This form also has a specific tendency of passing to a skeleton-free phase (Botaniska Notiser **1941:** 33. 1941). The skeleton disappeared after the normal form had been cultivated for several years, during which time the decreasing average apical length had been followed down to a

certain minimum size which had been reached without auxospore formation. The cause of this might be that the strains in question have, during cultivation, been obtained in clones which consequently lacked sexual partners, in this case necessary for the formation of auxospores. This is in contrast to the skeleton-free forms described by Richter, Bachrach, Geitler, and Stosch which were probably produced through environmental influence on the forms growing vegetatively.

The skeleton-free types, although not a part of the normal development, are of a great interest since they may show resemblance to the phylogenetic ancestors of diatoms, i.e. unicellular brown-colored algae without a silica skeleton. The common origin of the Bacillariophyta and Phaeophyta is thus likely.

The morphologic results have as yet been presented only as preliminary communications but the author hopes to be able to issue a more complete and definite report of these parts of his investigations.

An interesting feature in the physiologic investigation was the demonstration of antagonism between the sulphanilamides and p-aminobenzoic acid (Naturwiss. **29:** 455. 1941; Science **94:** 389. 1941; Botaniska Notiser **1941:** 375. 1941). This is the first time that such an antagonism was found to exist in other organisms than bacteria. According to Fildes' theory (Lancet **238:** 955. 1940), p-aminobenzoic acid is thus also an essential metabolite for these autotrophic algae. In the experiments on the antagonism between sulphanilamides and p-aminobenzoic acid, it appeared that sulphanilamide inhibited growth more than sulphapyridine, which was in its turn more growth inhibiting than sulphathiazole. In the presence of p-aminobenzoic acid, however, conditions were the reverse. From this it was interpreted that sulphapyridine and sulphathiazole also influenced other biochemical processes than those connected with the p-aminobenzoic acid (cf. Nature **150:** 290. 1942). This opinion has found support in observations of other experiments with other organisms (West, Proc. Soc. Exp. Biol. Med. **46:** 369. 1941; Dorfman & Koser, Journ. Infect. Dis. **71:** 241. 1942; Teply et al, Journ. Pharmacol. **77:** 207. 1943).

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NEW AND NOTEWORTHY PHILIPPINE MOSSES

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Since the "Mosses of the Philippines" was published in 1939, several important and quite extensive collections have added a number of significant species to the local moss flora which are here placed on record. In the following list of twenty-six species, seven are apparently new to science, twelve are species previously unrecorded from the Islands, and self-explanatory remarks accompany the remaining seven.

The supplementary collections from which these records are derived total well over 400 numbers. Only the more noteworthy collections are listed here but the remainder is important from the standpoint of local distribution. The collectors to whom we are indebted and the principal sources of the material are as follows: Luzon and Mindoro — Mr. José V. Santos in 1938; Mindanao, Palawan and Mindoro — Mr. Liborio E. Ebalo, 1939–1940; Mindanao — Mr. A. Lynn Zwickey, Expedition of the Arnold Arboretum, Harvard University, and the Botanical Garden of the University of Michigan, 1938. I am further obligated to Mr. Santos for his labors in packeting and labelling the specimens accumulated by the University of Michigan so that they would be available for study. The collections from Mindanao, Mindoro and Palawan are especially valuable as much field work remains to be done in these areas, especially Mindanao, and it may be long years before these prolific regions are again open to further exploration.

With these additions the Moss Flora of the Philippines is expanded to 531 species representing 184 genera. It is highly probable that the total will exceed 600 species when the possibilities of the Archipelago are more fully developed.

The types of the new species are in the writer's herbarium and in the herbarium of the University of Michigan. A complete set of the series collected by Mr. Zwickey in Mindanao including the duplicate types will also be found in the Farlow Herbarium, Harvard University.

FISSIDENTACEAE

Fissidens (Crispidium) **Zwickeyi** Bartr. sp. nov. FIG. 1–4.

Dioicus. Caulis 5 mm. altus. Folia circa 10 juga, sicca falcato-flexuosa, oblongo-ovata, obtusa, breviter apiculata, ad 1.6 mm. longa, 0.5 mm. lata, elimbata, lamina dorsalis ad basin costae rotundata, margines ubique crenulati, cellulae hexagonae, chlorophyllosae, laevissimae, diam. 10 μ, costa percurrens vel infra apicem soluta. Fructus terminalis, seta 2–3 mm. alta, superne arcuata, theca inclinata, deoperculata 0.8 mm. longa, sicca sub ore contracta.

Mindanao: Lanao Prov., vicinity of Olangu near Momungan, alt. 400 - 500 m., in thin layer of clay on moist rock, 25 Nov. 1938, *A. L. Zwickey, 838.*

Near *F. sylvaticus* Griff. but I think clearly distinguished from this species by the more broadly pointed leaves, the essentially smooth lamina cells and the inclined or horizontal capsules.

Fissidens lagunensis Bartr. nom nov.

Fissidens diversiretis Bartr. Philipp. Journ. Sci. **68** (1–4): 21. 1939.

I find that the name *Fissidens diversiretis* was used twice prior to its publication in the "Mosses of the Philippines." Brotherus describes *F. diversiretis* from Yunnan Prov., China[1] followed by *F. diversiretis* Dixon from Fiji[2] in 1930. Since *F. diversiretis* Broth. has priority, I propose the above new name for the Philippine plants.

Fissidens Wichurae Broth. & Fleisch. Hedw. **38**: (127). 1899.

Mindanao: Lanao Prov., vicinity of Dansalan, alt. 700–800 m., on clay hummock, forest floor, Nov. 23, 1938, *A. L. Zwickey, 794.*

New to the Philippine Islands.

Distribution: Java.

DICRANACEAE

Angstroemia orientalis Mitt.

Luzon: Mountain Prov., Mt. Data, 26 March 1938, *José V. Santos, 937a,* in part.

Previously known in the Philippines from only a single locality on Mt. Pulog.

LEUCOBRYACEAE

Leucophanes Massarti Ren. & Card. Rev. Bryol. **23**: 99. 1896.

Mindanao: Lanao Prov. Ulango Mountain, on bark of tree, 26 Feb. to 30 March 1941, *Liborio E. Ebalo, 1176.*

New to the Philippine Islands.

Distribution: Java.

This collection, which matches almost exactly Fleischer's Musc. Frond. Arch. Ind. no. 205 from Java, is distinguished by the longer leaves (7–9 mm.) in contrast to the short leaves (3–6 mm.) of *L. octoblepharioides* Brid.

CALYMPERACEAE

Syrrhopodon hispido-ciliatus Bartr. nom. nov.

Syrrhopodon perarmatus Bartr. Farlowia **1** (1): 42. 1943 non *Syrrhopodon perarmatus* Broth. Journ. Proc. Roy. Soc. N. S. Wales **49**: 133. 1915.

Mindanao: Zamboanga Prov., Muralong Mountain near Kabasalan, on dead log, 27 Nov. 1940, *Liborio E. Ebalo, 737.*

New to the Philippine Islands.

Distribution: New Guinea.

Mr. Dixon has kindly called to my attention that the name *S. perarmatus* is preoccupied by a New Hebrides moss as indicated above, hence the change.

It is an interesting coincidence that this species should turn up in Mindanao so soon after its discovery in Papua, New Guinea. It will be

[1] Symbolae Sinicae, Part IV, p. 11, 1929.

[2] Proc. Linn. Soc. N. S. Wales **55** (3): 270. 1930.

readily separated from *S. philippinensis* Bartr. by the narrower, rigidly erect-spreading leaves acute at the apex and the more densely hispid costa.

Calymperes porrectum Mitt. Linn. Soc. Journ. (Bot.) **10**: 172. 1869.

Calymperes salakense Besch. Ann. Sci. Nat. ser. 8. **1**: 302. 1895.

Mindanao: Lanao Prov., vicinity of Dansalan, alt. 700–800 m., on trunk of tree, Oct. 6, 1938, *A. Lynn Zwickey, 268.*

Distribution: Malakka, Java, New Guinea, Samoa.

A recent study of some Samoan collections indicates that *C. porrectum* Mitt. and *C. salakense* Besch. are identical. As Mitten's name has unquestioned priority I am reducing *C. salakense* to synonymy.

When the "Mosses of the Philippines" was published I had seen no material of this species from the local area. The Mindanao collection is a robust form showing the upper leaf margins coarsely and distantly toothed, the teniolae well in at the leaf shoulders and the cancellinae slightly rounded above, but these variations are of slight importance. In all the material of this species that I have seen, the abnormal leaves are mixed with the normal ones and reduced above to a bare costa which is gemmiferous at the tip, suggestive of pseudopodia.

Calymperes strictifolium (Mitt.) Roth, Hedwigia **51**: 127. 1911.

Syrrhopodon strictifolius Mitt. in Seemann Fl. Vit. p. 388. 1873.

Syrrhopodon tuberculosus Dix & Ther. Journ. Linn. Soc. (Bot.) **43**: 303. 1916.

Mindanao: Lanao Prov., vicinity of Davis Falls, alt. 200–300 m., moist crevices and beneath "overhangs" of rocks, 29 Oct. 1938, *A. Lynn Zwickey, 552.*

Distribution: Borneo, Fiji, Samoa.

Comparison with a part of the type collection of *Syrrhopodon strictifolius* Mitt. fails to reveal any practical distinctions between this species and *Calymperes tuberculosum* (Dix. & Ther.) Broth. so there is no alternative but to reduce the latter name to synonymy.

Calymperes (Eucalymperes) **Ebaloi** Bartr. sp. nov. FIG. 5–10.

Caespites densi, sordide virides, haud nitidi. Caules brevissimi, 4–8 mm. alti, dense foliosi. Folia sicca et humida erecta, leniter flexuosa, haud contorta, ad 16 mm. longa, e basi breve ovata longe et anguste ligulata, limbata, sensim late acuta, vix 0.25 mm. lata, lamina inferne sensim contracta, longe supra basin angustissima vel nulla; marginibus ubique et remote denticulatis, ad basin dense spinoso-serratis; costa valida, percurrente, dorso ad apicem solum denticulata; cellulae superiores laevissimae, subquadratae, diam. 10–12 μ; cancellina bene definita, supra acutata, teniola ad basin indistincta, in lamina validiuscula, fere ad apicem attingens, intromarginata. Seta tenuis 12 mm. longa, laevis; theca cylindrica, deoperculata 1.5 mm. longa. Caetera ignota.

Mindanao: Zamboanga Prov., Lilimbrog Mountain near Kabasalan, on tree trunk, 24 Nov. 1940, *Liborio Ela Ebalo, 664.*

Widely distinct from *C. serratum* A. Br. in the petiole-like base, the intramarginal leaf border and the straight or only slightly flexuose leaves. I have an undescribed species from Fiji with similar leaves in which the

lamina is gradually contracted below to a stretch of bare costa, then widened abruptly again at the shoulders of the leaf base, but in the Fiji plants the leaves are shorter without an intramarginal border, the lamina cells papillose and the leaf shoulders not spinose-serrate.

MNIACEAE

Orthomniopsis japonica Broth. Ofv. Finska Vet.-Soc. Forh. **49** (10): 1. 1905–06.

Luzon: Bontoc Subprov., June–July 1911, *Father M. Vanoverbergh, 1282.*

Distribution: Assam, New Guinea, Japan.

Through the kindness of Dr. Quisumbing I have seen part of the above collection which is unquestionably this species. For some reason it was not included in the material sent from the Bureau of Science as a basis for the study of the local moss flora.

BARTRAMIACEAE

Philonotis evanidinervis Fleisch. Laubmoosfl. Java **2**: 412. 1902–04.

Mindanao: Lanao Prov., vicinity of Dansalan, alt. 700–800 m., on rock, edge of stream, secondary forest toward Remain, 28 October 1938, *A. Lynn Zwickey, 539.*

New to the Philippine Islands.

Distribution: Java.

An interesting extension of this localized species previously known only from several localities in West Java.

RHACOPILACEAE

Rhacopilum magnirete Bartr. sp. nov. FIG. 11–14.

Sat robustum, caespites late extensi, lutescentes, haud nitidi. Caules intertexti, fere ad apicem dense rufo-tomentosi, irregulariter ramosi. Folia late ovata, acuta, breviter cuspidata, 2 mm. longa, 1 mm. lata. sicca fortiter inflexa, humida late patentia; margines plani, supra medium irregulariter denticulati; costa tenuis, superne valde angustiora, sensim in cuspidem attenuata, saepe infra apicem dissoluta; cellulae superiores majusculae, pellucidae, laeves, hexagonae, 22–25 μ longae, parietibus firmis, basin versus paullo majores, internae longiores. Amphigastria multo minora, ovato-lanceolata, sensim acuminata, costa longe excurrente. Caetera ignota.

Mindanao: Lanao Prov., Saguiran Mountain, on tree trunk, 26 Feb. to 30 March 1941, *Liborio E. Ebalo, 1124.*

This species is possibly nearest *R. Schmidii* (C. M.) Jaeg. but the densely tomentose stems, more coarsely toothed leaves, the slender costa ending in the shorter point or even disappearing below the apex, together with the larger pellucid and distinct upper leaf cells are distinctive features. From *R. spectabile* Reinw. & Hsch. it will be separated by the less robust habit, larger lamina cells, less coarsely toothed leaf margins and the absence of the area of lax juxtacostal cells in the leaf base.

THUIDIACEAE

Herpetineurum toccoae (Sull. & Lesq.) Card. Beihefte Bot. Centralb. **19** (2): 127. 1905.

Anomodon toccoae Sull. & Lesq. Musc. Bor. Am. (Ed. 1) no. 240. 1856.

Luzon: Malinao, Atimanan, Tayabas Prov., on ground, 25 Oct. 1927, *José V. Santos, 862.*

New to Philippine Islands.

Distribution: Africa, Asia, Ceylon, Sumatra, Java, Celebes, New Caledonia, Formosa, South America, Guatemala, Mexico, Southern United States.

It is not surprising to find this almost cosmopolitan species in the Philippines. Although not common anywhere it seems to occur sporadically in temperate and tropical regions throughout the world.

PTEROBRYACEAE

Endotrichella nematosa Bartr. sp. nov. FIG. 15–17.

Robusta, flavescens, nitida. Caules secundarii ad 5 cm. alti, complanati, densifolii, circa 8 mm. lati, superne saepe attenuati et prope apicem propagula numerosa aurantiaca filiformia articulata instructi. Folia 5 mm. longa, 1.5 mm. lata, oblongo-lanceolata, ecostata, plicata, parum auriculata, in acumen cuspidatum raptim angustata; margines infra recurvi, superne distanter fortiter serrati, cellulae superiores anguste rhomboideae, perincrassatae, basilares lineares, infimae fuscae, fortiter porosae, alares oblongae, laxae, numerosae. Perichaetium parvum; theca exserta, leniter inclinata, deoperculata breviter oblonga, 1.8 mm. longa, 1 mm. lata; seta circa 2 mm. longa. Caetera ignota.

Panay: Mt. Bulilao, Capiz Prov., June 1919, *A. Martelino & G. Edano, 35812a.* Caroline Islands: Ponape Island, Kuporujo, grows on top of the mountain on epiphytic orchid, 13 March 1936, Masahiko Takamatsu, Herb. B. P. Bishop Museum, 661a (TYPE).

An outstanding species in the caudate tips of the secondary stems which are abundantly felted with erect, filiform, orange-brown, articulated brood filaments as in some of the species of *Cyathophorella.*

Garovaglia Zwickeyi Bart. sp. nov. FIG. 18–20.

Rigida, aureo-viridis, nitidula. Caules circa 4 cm. alti, sat gracili. Folia dense conferta, erecta, arcte appressa, late orbiculato-ovata, haud undulata, fortiter plicata, breviter cuspidata, 2.5 mm. longa, 2 mm. lata; margines plani, leniter denticulati; costae nullae; cellulae breviter rhomboideae, parietibus firmis, alares rectangulares, numerosae. Perichaetium longe exsertum, folia perichaetialia abrupte breviter cuspidata, superne erosa, theca immersa. Caetera ignota.

Mindanao: Lanao Prov., vicinity of Olangu near Momungan, alt. 400–500 m., on trunk of tree, 10 November 1938, *A. Lynn Zwickey, 700.*

A very distinct species in the short, broad, closely appressed leaves giving the rather slender, subterete stems a catenulate appearance due to the reflexed upper leaf margins. It may be compared in a broad way with *G. rigida* Dix. of Siam but is widely different in the much shorter and relatively broader erect appressed leaves with the margins weakly denticulate.

NECKERACEAE

Neckeropsis nitidula (Mitt.) Fleisch. Laubmoosfl. Java **3**: 882. 1906–08.

Luzon: Tayabas Prov., Danlagan, Guinayagan, on tree branch, 19 Oct. 1936, *José V. Santos, 482.*

New to Philippine Islands.

Distribution: China, Japan, Formosa, Tonkin.

Notwithstanding my remarks on page 245 of the "Mosses of the Philippines" I am happy to definitely record the presence of this species in the local area.

Pinnatella ambigua (Bryol. Jav.) Fleisch.

Mindoro: Pandan Mountain, Bulalacao, on stone, 6–11 Nov. 1939, *Liborio E. Ebalo, 239.*

Distribution: Bhota, Burma, Sumatra, Java.

Although the plates in the "Bryologia Javanica" representing *P. ambigua* and *P. Kuhliana* respectively show clearly the distinctive difference in the shape of the stem leaves, unfortunately I failed to grasp this distinction when studying the Philippine collections and as a result confused the two species. *P. ambigua* is at once distinguished by the stem leaves gradually narrowed from an ovate base to a relatively slender acuminate point in bold contrast to the oblong-ovate abruptly short-pointed leaves of *P. Kuhliana.*

P. ambigua is apparently rare in the Philippines. Fleischer cites a collection from Luzon in the Laubmoosfl. Java, p. 919 but the only specimen I have seen is the one cited above.

Pinnatella Kuhliana (Lac.) Fleisch. Hedwigia **45**: 80. 1906.

New to the Philippine Islands.

Distribution: Sumatra, Java, Ceram, Celebes, New Guinea, Fiji, Samoa, Tahiti.

As explained above the description, figures and collections given under the heading of *P. ambigua* in the "Mosses of the Philippines" should all be referred to *Pinnatella Kuhliana.* This species does not seem to have been recorded from the Philippines but a careful check of all the available specimens shows that it is widely distributed throughout the archipelago and decidedly more frequent than *P. ambigua.*

Pinnatella mucronata (Lac.) Fleisch. Hedwigia **45**: 50. 1906.

Palawan: Tagbarungis Mt., vicinity of Puerto Princesa, on tree trunk, 14 February 1940, *Liborio E. Ebalo, 489.*

New to the Philippine Islands.

Distribution: Sumatra, Java, Borneo, Ceram, Celebes, New Guinea, Samoa.

HOOKERIACEAE

Daltonia armata Bartr. sp. nov. FIG. 21–24.

Pallide viridis, nitidula. Caulis ad 1 cm. altus. Folia 3.5 mm. longa, 1 mm. lata, oblongo-ovata, longe piliformiter aristata, erecto-patentia, sicca leniter contorta, ubique angustissime limbata, integerrima; costa tenuissima, vix dimidiam partem folii attingens; cellulae superiores elongate hexagonae, 40–60 x 10–16 μ, parietibus tenuiusculis, basilares lineares. Seta 3 mm. longa, fere ad basin argute tuberculosa; theca erecta, deoperculata 1.2 mm. longa; calyptra fimbriata.

Mindanao: Lanao Prov., vicinity of Dansalan, alt. 700–800 m., on culm of climbing bamboo, Sacred Mountain, 3 Nov. 1938, *A. Lynn Zwickey, 638.*

The leaves of *D. armata* are similar in shape to those of *D. aristifolia* Ren. & Card. of Java but the resemblance ends here. In *D. armata* the upper lamina cells are oval-hexagonal up to 60 μ long and the setae are densely armed throughout with high tubercular-like spines up to 25 μ high.

PLAGIOTHECIACEAE

Plagiothecium neckeroideum Br. & Schp. var. **javense** Fleisch. Laubmoosfl. Java **4:** 1168. 1920.

Luzon: Mountain Prov., Mt. Pawai, Benguet, on ground, 27 March 1938, *José V. Santos, 1035.*

Distribution: Sikkim, Java.

In this collection the setae are 3–4 cm. long, thus agreeing with the description of Fleischer's var. *javense.* In the absence of any other well marked differences it seems probable that the variety is hardly more than a robust form of the species.

SEMATOPHYLLACEAE

Heterophyllum Santosii Bartr. sp. nov. FIG. 25–28.

Autoicum, pallide aureum, nitidum. Caulis prostratus, elongatus, regulariter pinnatim ramosus, ad 9 cm. longus, ramis vix 1 cm. longis, leniter flexuosis, apice falcato. Folia caulina falcata, 2.5–3 mm. longa, e basi late oblonga raptim linearilanceolata, superne spinoso-serrata; marginibus inferne integris, anguste revolutis; costa bina, brevissima; cellulae superiores lineares, parietibus, hyalinis, firmis, basilares longiores, angustiores, infimae laxiores, fuscae, valde porosae, alares numerosae, oblongae, hyalinae vel fuscae, haud vesiculosae. Folia ramea minora, breviora, angustiora, sensim acuminata, argute serrata, apicem versus saepe rugoso-undulata. Seta 37 mm. longa, rubella, superne tenuissima; theca suberecta, deoperculata 2.5 mm. longa. Caetera ignota.

Luzon: Mountain Prov., Mt. Data, Benguet, on tree trunk, 26 March 1938. *José V. Santos, 957.*

A splendid species, possibly allied to *H. brachycarpum* (Mitt.) Fleisch. of Japan but widely different in the elongated stems regularly and closely pinnate forming narrow fronds when moist. The unusually long seta shown by the only available sporophyte is also a distinctive feature. The genus adds a new and interesting element to the local flora from a region which has been carefully worked over by many previous collectors, so Mr. Santos may well be proud of his discovery.

Glossadelphus similans (Bryol. Jav.) Fleisch. E. & P. Nat. Pflanzenfam. Musci p. 1093. 1908.

Luzon: Mountain Prov., Mt. Pawai, Benguet, on dead log, 27 March 1938, *José V. Santos, 1027.*

New to Philippine Islands.

Distribution: Java.

Glossadelphus hermaphroditus Fleisch. Laubmoosfl. Java **4**: 1359. 1920.

Mindanao: Lanao Prov., vicinity of Guassi-Dansalan Road, alt. 700–800 m., on boulder in stream bed near Togaya, 2 Nov. 1938, *A. Lynn Zwickey, 618.*

New to Philippine Islands.

Distribution: Java.

Pseudohypnella verrucosa (Doz. & Molk.) Fleisch. Laubmoosfl. Java **4**: 1368. 1921.

Mindanao: Lanao Prov., Mt. Makaturing, alt. 800–1000 m., on rotting wood, 22 Oct. 1938, *A. Lynn Zwickey, 489.*

New to Philippine Islands.

Distribution: Ceylon, Java, Banka.

POLYTRICHACEAE

Pogonatum macrophylloides Broth. Mitt. Inst. allgem. Bot. **7** (2): 140. 1928.

Luzon: Mountain Prov., Mt. Pawai, Benguet, on ground, 27 March 1938, *José V. Santos, 1026.*

New to Philippine Islands.

Distribution: Borneo.

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EXPLANATION OF PLATE

Fig. 1–4. *Fissidens Zwickeyi* Bartr.

1. Plants × 1.
2. Leaf × 20.
3. Apex of leaf × 200.
4. Capsule × 7.

Fig. 5–10. *Calymperes Ebaloi* Bartr.

5. Plant × 1.
6. Leaf × 4.
7. Apex of leaf × 50.
8. Leaf base × 20.
9. Upper cells and margin × 200.
10. Part of cross section from upper half of leaf × 200.

Fig. 11–14. *Rhacopilum magnirete* Bartr.

11. Part of plant × 1.
12. Leaf × 15.
13. Apex of leaf × 40.
14. Upper leaf cells and margin × 200.

Fig. 15–17. *Endotrichella nematosa* Bartr.

15. Plant × 1.
16. Part of propagulum × 200.
17. Leaf × 7.

Fig. 18–20. *Garovaglia Zwickeyi* Bartr.

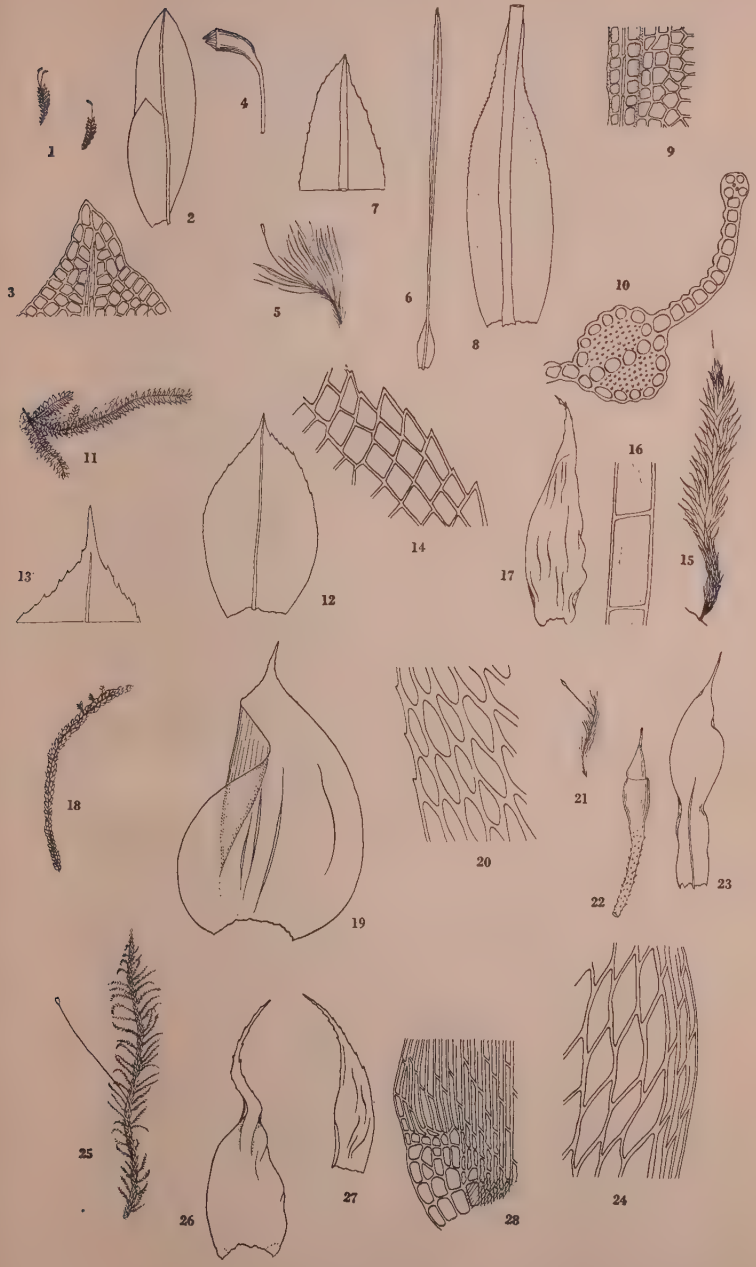
18. Plant × 1.
19. Leaf × 16.
20. Upper leaf cells and margin × 200.

Fig. 21–24. *Daltonia armata* Bartr.

21. Plant × 1.
22. Capsule × 9.
23. Leaf × 10.
24. Upper leaf cells and margin × 200.

Fig. 25–28. *Heterophyllum Santosii* Bartr.

25. Plant × ½.
26. Stem leaf × 13.
27. Branch leaf × 13.
28. Basal angle of leaf × 80.



FIGURES 1–28

1(4): 515–523 FARLOWIA July, 1944

ON TWO NEW SPECIES OF MEGACEROS WITH NOTES ON M. ARACHNOIDEUS, M. DENTICULATUS, M. GIGANTEUS, AND M. GRANDIS

L. P. Khanna

For the material which forms the basis of this note, the writer is indebted to Mrs. E. A. Hodgson, Wairoa, P. O. Hawkes Bay, New Zealand, to whom he wishes to express his thanks. Thanks are also due to Dr. Eduardo Quisumbing, Curator, Philippine National Herbarium, Manila, and to Dr. R. E. Holttum, Director, Botanical Gardens, Singapore, for the loan of specimens from their herbaria.

Megaceros Hodgsoniae sp. nov. FIGS. 1–6.

Planta monoica. Sectio transversa 5–6 cellis excelsitato, solida. Cellae superficiales 30–70 × 25–45 μ. Involucre geminatum, 5–6 mm. longitudine, 0.5 1.5 mm. latitudine, cylindricum, attenuatum. Capsula 8–15 mm. longitudine, 0.25–0.35 mm. latitudine. Sporae pallidae, verrucolosae, 30–40 μ.

Monoecious. In patches. Thallus up to 25 mm. long, nearly flat, smooth, divided into broad obovate lobes, more or less rounded at the apex with margin nearly entire; transverse section 5–6 cells high in the middle, without lacunae; surface cells 30–70 x 25 45 μ. Involucre frequently geminate, 5–6 mm. long and 0.5–1.5 mm. broad, cylindrical, slightly narrowing at truncate apex. Capsule 8–15 mm. long and 0.25–0.35 mm. broad, wall cells thickened, light brown. Spores 30–40 μ, pale, verrucose. On Popa Rock in creek in deep shade, Kiwi, April, 1935.

From the comparative chart of the species of *Megaceros* Campbell 1907 appended, the following species agree with the form described in having the verrucose type of spore surface: *M. arachnoideus* Stephani 1916, *M. denticulatus* (Lehman 1857) Stephani 1916, *M. juegiensis* Stephani 1923, *M. martinicensis* Stephani 1916. The present form differs from *M. martinicensis* by the shorter capsule and the larger thallus, from *M. arachnoideus, M. denticulatus* and *M. juegiensis* by the shorter capsule and the structure of the thallus. It is therefore necessary to create a new species for which the name *M. Hodgsoniae* is suggested.

Megaceros Zotovii sp. nov. FIGS. 7–10.

Planta monoica. Sectio transversa 10–12 cellis excelsitato, solida; cellae superficiales 30–45 x 15–25 μ. Involucre solitarium, cylindricum, attenuatum, 12 16 mm. longitudine, 1.5–2 mm. latitudine. Capsula 40–60 mm. longa, 0.5 mm. lata. Sporae pallidae, verruculosae, 30–35 μ.

Monoecious. In patches, light green. Thallus up to 50 mm. in diameter, fan-shaped, with obovate lobes, rounded at the apex with margin finely crenate, transverse section 10–12 cells high in the middle, without lacunae; dorsal epidermal cells 30–45 x 15–25 μ. Involucre 12–16 mm. long and 1.5–2 mm. broad, cylindrical, narrowing towards the nearly truncate apex. Capsule 40–60 mm. long and 0.5 mm. broad. Spores 30–35 μ, pale, somewhat irregular in shape, verrucose. Elators unbranched, 0.2–0.3 mm. long. Epidermal cells of the capsule somewhat

thickened. Cehatorawa Saddle, Tarama Mts., New Zealand, 26 Nov. 1933, *V. D. Zotov.*

The above described species agrees with the following in having verrucose spores: *M. arachnoideus* Stephani 1916, *M. denticulatus* (Lehmann 1857) Stephani 1916, *M. fuegiensis* Stephani 1923, *M. Hodgsoniae* Khanna and *M. martinicensis* Stephani 1916. The present form differs from *M. denticulatus* and *M. Hodgsoniae* by its longer involucre and capsule, from *M. arachnoideus, M. fuegiensis* and *M. martinicensis* by the bigger involucre and other characters of the thallus.

Megaceros giganteus (Lehmann et Lindenberg) Stephani FIGS. 11–15.

Monoecious. In light green patches. Thallus up to 50 mm. in diameter, divided into obovate lobes, depressed in the center, margin slightly ascending-irregular; transverse section 8-10 cells high in the middle, without lacunae; surface cells 8–20 x 20-30 μ. Involucre 8 15 mm. long and 1.0–1.5 mm. broad, cylindrical, slightly narrowed towards the apex, the mouth lobulate. Capsule 40–60 mm. long and 0.4–0.8 mm. broad, epidermal cells of the capsule, long, narrow, highly thickened, and some cells with brownish contents. Spores 30–35 μ, pale, asperulate. Elators long and slender, sometimes 0.5 mm. in length, unbranched. Antheridia singly on prominent stalks. Water course, north of Field Flat, 8 Oct. 1933, *V. D. Zotov.*

The above described species agrees with the following in having the same type of spore surface: *M. caledonicus* Stephani 1916, *M. celebensis* Stephani 1916, *M. crassus* Stephani 1916, *M. endiviaefolius* (Montagne 1856) Stephani 1916, *M. giganteus* (Lehmann et Lindenberg 1834) Stephani 1916, *M. Jamesonii* (Taylor 1848) Stephani 1916, *M. lacerus* (Nees 1844) Stephani 1916, *M. longispirus* (Carrington & Pearson 1887) Stephani 1916, *M. monandrus* Stephani 1916, *M. Novae-guineae* Stephani 1916, *M. Novae-zelandiae* Stephani 1916, *M. pallens* (Stephani 1892) Stephani 1916, *M. parvisporus* Stephani 1916, *M. solidus* Stephani 1916.

The present species differs from *M. caledonicus, M. celebensis, M. crassus, M. lacerus, M. monandrus, M. Novae-guineae, M. pallens,* and *M. solidus* by the larger thallus and involucre; from *M. endiviaefolius* by its shorter capsule; from *M. Jamesonii* by its smaller spore and other vegetative characters; from *M. lacerus* by the shape and the other characters of the thallus. *M. giganteus, M. Novae-zelandiae* and *M. parvisporus* and the above described species differ from each other in minor characters which are not sufficiently distinct to be of specific value. The writer therefore is of the opinion that these may be considered as a single species — *M. giganteus* (Lehman et Lindenberg 1834) Stephani 1916.

The writer has been unable to consult Stephani's material of these forms and is therefore unable to state whether differences exist which would supplement the already existing description. Judging from the characters so far given, however, he is of the opinion that there is only one species, and the other two listed are environment forms without specific validity.

Megaceros grandis (Angstrom) Stephani FIGS. 16–20.

Monoecious. On rotten log, mixed with mosses. In light green patches. Thallus 12–20 mm. in diameter, fan-shaped or nearly so; slightly depressed in the center, the margin ascending; divided into numerous narrow linear lobes, dorsal surface rough with several fine lamellae; surface cells 35–55 x 20–40 μ, transverse section 5 cells high in the middle, without lacunae. Involucre 4.5–6.5 mm. long and 0.8–1.0 mm. broad, cylindrical, narrowing to the almost truncate apex. Capsule 12–40 mm. long and 0.3–0.5 mm. broad, epidermal cells long, thick-walled. Spores 25–35 μ, pale green, granular; elators unbranched, 0.18–0.2 mm. long. Antheridia borne singly in the antheridial cavity. Stream side — on a log in a bush about 3000 ft. above sea level; on Tauhara, New Zealand.

From the comparative chart of *Megaceros* Campbell, 1907, the following species agree with that described above in having the same type of spore surface: *M. grandis* (Angstrom 1873) Stephani 1916, *M. vescoanus* Stephani 1916, *M. vincentianus* (Lehmann et Lindenberg 1834) Stephani 1916.

The present species can be separated from *M. vincentianus* by its shorter capsule and other structures of the thallus; *M. grandis*, *M. vescoanus* and the above differ from each other in minor characters which are not sufficiently distinct to be of specific value. The writer, therefore, is of the opinion that these may be considered as a single species — *M. grandis* (Angstrom 1873) Stephani 1916.

Megaceros denticulatus (Lehmann) Stephani FIGS. 21–25.

Monoecious. In overlapping patches. Thallus variable, up to 55 mm. long and 40 mm. broad, with irregular branches, rounded at the apex, with margin irregular; from the ventral surface marginal buds are given off; the upper superficial cells 25–30 x 10–20 μ. Involucre 5–7 mm. long and 0.8 mm. broad, narrowing towards the apex, the mouth lobulate. Capsule 16–20 mm. long and 0.5 mm. broad, brownish. Spores 35–40 μ, pale yellow, verrucose. Capsule wall cells highly thickened.

From the description this plant appears to be *M. denticulatus* (Lehmann 1857) Stephani 1916 — though the present form differs by the larger involucre and the smaller spores — but these differences within a narrow limit are not sufficiently distinct to be of specific value.

Megaceros arachnoideus Stephani FIGS. 26–29.

Monoecious. In patches. Thallus 15 mm. in diameter, divided into broad obovate lobes, with margin lacerate; dorsal surface rough with several leaf-like lamellae; transverse section 10–14 cells high in the middle, without lacunae; upper superficial cells 35–45 x 20–45 μ. Involucre 6–10 mm. long and 0.6–1.2 mm. broad, narrowing towards the apex, mouth lobulate. Capsule 25–35 mm. long and 0.3–0.4 mm. broad, brownish. Spores 25–40 μ, somewhat irregular in shape, greenish yellow, verrucose. Elators long and slender, sometimes 0.2 mm. in length. On damp earth by creek by [Mols St. ?] New Zealand, 26 Dec. 1932, E. A. Hodgson.

This form agrees with *M. arachnoideus* Stephani 1916 but shows minor differences.

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APPENDIX

SPECIES OF MEGACEROS

	Size of plant mm.	*Involucre* mm.	*Capsule* mm.	*Spore*	*Distribution*
alatifrons Steph.	20 x 3	7	30	27 μ, small papillae in center	Brazil
amoenus Steph.	20 x 3	7	30	27 μ, umbonate	Guadeloupe
aneuraeformis Steph.	40 x 5	5	30	36 μ, umbonate	Brazil
arachnoideus Steph.	40 x 25	7	30	36 μ, yellow, verrucose	New Zealand
caledonicus Steph.	20 x 3	5	40	27 μ, minutely asper	New Caledonia
callistictus Steph.	20 x 3	3	15	22 μ, muricate	Brazil
carnosus Steph.	30	5	50	27 μ, yellow, muricate	Australia
celebensis Steph.	20 x 12	8	30	27 μ, minutely asper	Celebes
columbianus Steph.	15 x 5	12	40	36 μ, umbonate	Colombia
crassus Steph.	20	6	40	36 μ, asper	Tasmania
cristisporus Steph.	40	15	70	27 μ, yellow, papillate	Costa Rica
denticulatus (Lehm.) Steph.	50	2	20	45 μ, yellow, verrucose	New Zealand
endiviaefolius (Mont.) Steph.	60 x 7	7	90	36 μ, asper	Chile
flagellaris (Mitt.) Steph.	40 x 5	7	40	18 μ, muricate	Fiji
flavens (Spruce)	30 x 5	8	60	27 μ, muricate	Peru
fuegiensis Steph.	30 x 8	5	40	36 μ, verrucose	Tierra del Fuego
giganteus (Lehm. & Lindenb.) Steph.	45 x 7	10	40	27 μ, asper	New Zealand
gracilis (Reichardt) Steph.	20	5	40	36 μ, papillate	Australia
grandis (Angstr.) Steph.	30 x 10	10	30	27 μ, granulate	Tahiti
guatemalensis Steph.	40 x 5	9	60	27 μ, papillate	Guatemala
jamaicensis Steph.	50 x 10	10	40	27 μ, papillate	Jamaica
Jamesonii (Tayl.) Steph.	40 x 10	10	50	54 μ, asper	Peru
lacerus (Nees) Steph.	40	7	40	36 μ, asper	Africa
laciniatus (Schw.) Steph.	40	5	40	— μ, muricate	Mexico
leptohymenius (Tayl.) Steph.	50 x 10	10	40	36 μ, papillate	New Zealand
longispirus (Carr. & Pears.) Steph.	50 x 20	5	50	36 μ, minutely asper	Tasmania
martinicensis Steph.	10 x 4	4	40	27 μ, dark, verrucose	Martinique
mexicanus Steph.	15 x 4	4	40	27 μ, papillate	Mexico
minarum (Nees) Steph.	20	5	40	27 μ, yellow, papillate	Brazil
monandrus Steph.	30	5	20	27 μ, minutely asper	Asia
monospirus Steph.	35	7	25	27 μ, papillate	New Caledonia
muriculatus Steph.	30	5	45	27 μ, muricate	New Caledonia
Novae-guineae Steph.	20 x 3	5	40	27 μ, asper	New Guinea
Novae-zelandiae Steph.	40	5	30	27 μ, asper	New Zealand
Nymanii Steph.	30	4	35	36 μ, papillate	New Guinea
pallens (Steph.) Steph.	25 x 5	5	40	27 μ, asper	New Zealand
parvisporus Steph.	30 x 5	10	40	18 μ, asper	Samoa
salakensis Campb.	30	6	40	28 μ, minutely echinate	Java
schizophyllus (Gottsche) Steph.	15	5	20	27 μ, tuberculate	Cuba
solidus Steph.	20 x 4	6	20	36 μ, asper	Guadeloupe
Stahlii Steph.	30	15	80	27 μ, yellow, densely papillate	Java
tjibodensis Campb.	50 x 15	10	90	27 μ, papillate	Java, Sumatra
tosanus Steph.	30	7	20	27 μ, muriculate	Japan
Vescoanus Steph.	40 x 7	7	40	18 μ, granular	Tahiti
vincentianus (Lehm. & Lindenb.) Steph.	40 x 6	5	50	27 μ, granular	Guadeloupe, St. Vincent
Wiemanii Steph.	20 x 10	15	50	27 μ, umbonate	Brazil

EXPLANATION OF FIGURES 1–15

In figures 1 and 11, the scale equals 1 millimeter; in all other figures the scale equals 20 μ.

Megaceros Hodgsoniae. Figs. 1–6.

1. Young plant showing sporophyte.
2. Dorsal epidermal cells.
3–4. Spores.
5. A portion of an elator.
6. Capsule wall cells.

Megaceros Zotovii. Figs. 7–10.

7. Dorsal epidermal cells.
8. Different views of spores.
9. Part of elator.
10. Capsule wall cells.

Megaceros giganteus. Figs. 11–15.

11. Thallus showing sporophyte.
12. Dorsal epidermal cells.
13. Spore.
14. Elator.
15. Capsule wall cells.

FIGURES 1–15

EXPLANATION OF FIGURES 16–29

In figures 16, 21, and 26, the scale equals 1 millimeter; in all other figures the scale equals 20 μ.

Megaceros grandis. Figs. 16–20.

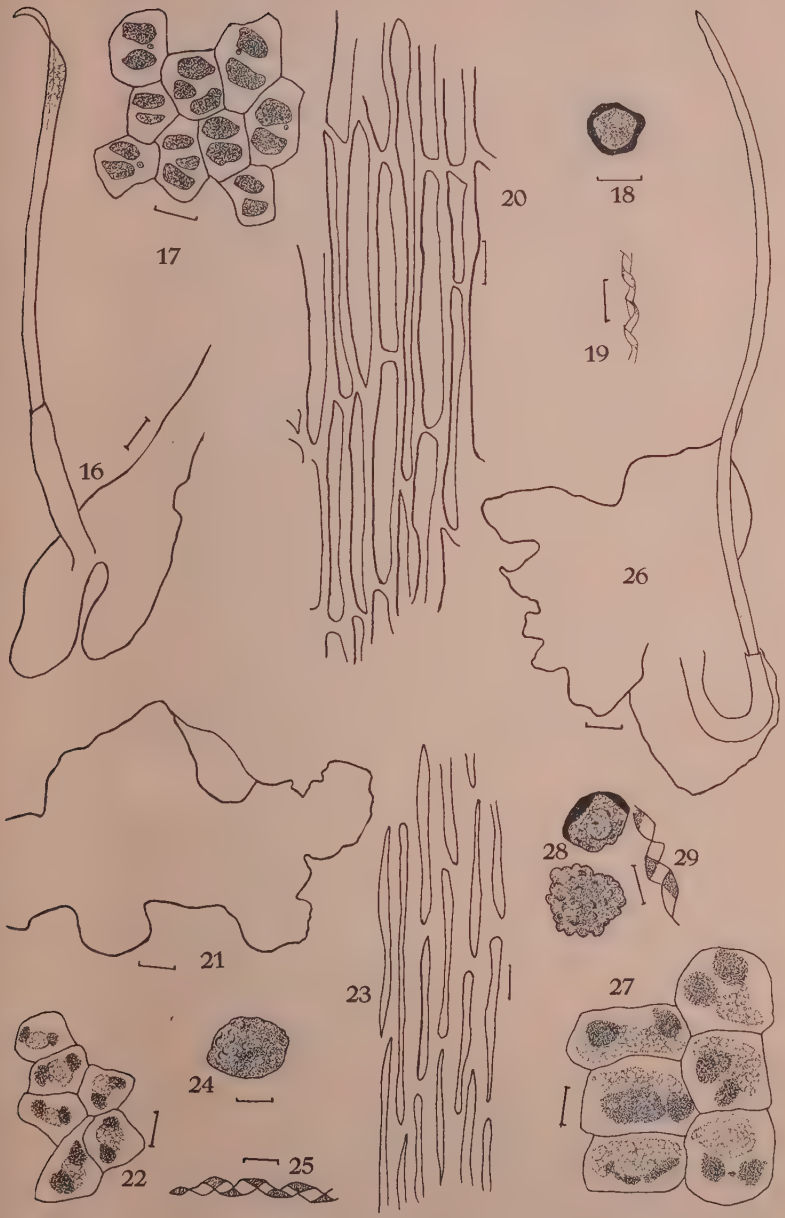
16. A young plant.
17. Dorsal epidermal cells of the thallus.
18. Spore.
19. A portion of an elator.
20. Epidermal cells of the capsule wall.

Megaceros denticulatus. Figs. 21–25.

21. A portion of the lobe of the thallus showing the irregular margin.
22. Epidermal cells of the thallus.
23. Capsule cell walls.
24. Spore.
25. Portion of an elator.

Megaceros arachnoideus. Figs. 26–29.

26. Young plant.
27. Dorsal epidermal cells of the thallus.
28. Spores.
29. A portion of an elator.



FIGURES 16–29

1(4): 525–568 FARLOWIA July, 1944

STUDIES ON POLYSTICTUS CIRCINATUS AND ITS RELATION TO BUTT-ROT OF SPRUCE

ROGER GOSSELIN[1]

During the writer's study of the butt-rots of spruces in the Province of Quebec, it was found that the most important fungi causing butt-rots are *Poria subacida*, *Polyporus balsameus*, *Polyporus Schweinitzii*, and *Polyporus circinatus*. This last was chosen for study because of the irregular occurrence of the species and of its importance locally in causing excessive windfall.

It soon became evident that what had been determined as *P. circinatus* actually included two distinct fungi. One was characterized by its brighter color and by the fact that it occurred chiefly on the ground; the other was characterized by the darker color of the sporophores and by the fact that it occurred mostly on the trunks of the trees. These differences between the two forms which were so obvious in the field, led to the investigations of the taxonomy. It was found that the two organisms could be separated microscopically by the character of the setae present in the hymenium and this led to their determination as *Polyporus tomentosus* Fr. and *Polyporus circinatus* Fr.

From a review of the literature it appears that there has been considerable confusion as to the identity of these two forms. This confusion has arisen since Fries described the two species, *P. tomentosus* in 1821 and *P. circinatus* in 1848, and it came from the fact that he described *P. tomentosus* as having a homogeneous context, yet according to specimens identified by Fries, both *P. tomentosus* and *P. circinatus* have a duplex context. The only difference, excepting the color and the shape, are the straight setae for the former and the predominantly curved setae for the latter.

Peck (1878) described a new species from New York, which he called *Polyporus dualis*. His species was sessile or short, lateral-stemmed and of rather dark color. Later, Ellis and Everhart (1889) examined specimens from Peck and found the curved setae characteristic of *P. circinatus* Fr. Cooke (1886) and Saccardo (1888) have given *P. dualis* Pk. as a synonym of *Polystictus circinatus* (Fr.) Cke. So it is fairly safe to say that Peck's type specimen is *P. circinatus* Fr.

In 1882, Karsten transferred *Polyporus tomentosus* to *Polystictus*. Later (1889) he segregated the new genus *Onnia* from *Polystictus*, placing emphasis upon the setal character of the hymenium. He distinguished *O. tomentosus* from *O. circinatus* by the homogeneous context of the former. Ellis and Everhart (1889) examined Karsten's specimen later and found straight setae for the plant he designated as *Onnia tomentosus*. Although Ellis and Everhart's illustration (1889) did not make this point

[1] Thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at Harvard University.

Contribution from the Laboratories of Cryptogamic Botany and the Farlow Herbarium, Harvard University, no. 225.

clear, Karsten's specimens show that there is a duplex context, hence his *Onnia tomentosus* is the same as *P. tomentosus* Fr. Little is known about his *O. circinatus*.

While Karsten was creating the genus *Onnia*, Ellis and Everhart (1889) created the genus *Mucronoporus* based on *Polyporus circinatus*. They described straight setae for *M. tomentosus* and curved ones for *M. circinatus*. Subsequent mycologists have considered these species synonymous with the two Friesian ones.

In 1900, Patouillard made a new genus *Xanthochrous* based on *P. circinatus*. He described the setae as being straight. Apparently his *X. circinatus* is *P. tomentosus* Fr.

Murrill (1904) refers to Fries' authentic specimens, stating that "the type of *Polyporus tomentosus* at Upsala corresponds in all respects with the plants found in America, having the same kind of spines and a dual context." Since Nannfeldt has reported in a personal letter to Haddow (1941) that there are no type specimens of either of Fries' species at Upsala, it is difficult to understand to which specimen Murrill refers. It is worth observing, however, that he attributed to his Friesian specimen of *P. tomentosus* a double context. Murrill (1916) comprises under the single species *Coltricia tomentosa* both *P. tomentosus* and *P. circinatus* of Fries.

There apparently was much confusion in Lloyd's mind in regard to the status of these two species. In 1908, he described *P. circinatus* Fr. as having straight setae, as in *P. tomentosus* Fr. Later in 1912, he stated that *P. tomentosus* Fr. was unknown from the United States and questioned whether *P. circinatus* Fr. was really distinct from *P. tomentosus* Fr., and finally suggested that "there are three (stipitate) forms of *Polyporus tomentosus* Fr.: first (typical), with thin context, straight setae; second (*circinatus*, American), thick context, straight setae; third (*circinatus*, European and American), curved setae."

Lloyd (1908), on account of the resemblance of *P. dualis* Pk. to Fries' figure of *P. triqueter*, suspected it to be *P. triqueter* of Europe. Bresadola, (1920) following Lloyd's opinion, considered *P. dualis* Pk. to be a synonym of *P. triqueter* Fr. Fries described *P. triqueter* in 1838, while *P. circinatus* was described only in 1848. He did not mention any relationship between the two species, hence *P. triqueter* Fr., if different from *P. dualis* Pk. as seems likely, cannot be used as a synonym for *P. circinatus* and there is little need to consider it in this discussion.

Neuman (1914) reported *P. tomentosus* from Wisconsin but gave no description of the microscopic characters. He considered *P. dualis* as a synonym of *P. tomentosus* and for that reason the exactitude of his identification may be questioned.

Lloyd (1920) described a new species, *Polyporus peakensis* Lloyd, from a single specimen collected by Hedgcock at Pikes Peak in Colorado. Later, Shope (1931) stated it was conspecific with *P. circinatus* Fr.

Sartory and Maire (1922) believed that *P. circinatus* is only a variety of *P. tomentosus,* a point of view shared by Haddow (1941).

Konrad and Maublanc (1926) under *Fomes* (*Xanthochrous*) *circinatus* furnished a picture of curved setae and described it as straight or curved. We previously mentioned the same thing for the wood-loving forms we found in the field. It should be *P. circinatus* Fr. Bourdot and Galzin (1927) made the same observations on what they called *P. circinatus* Fr.

Shope (1931), Overholts (1933) and Lowe (1934) followed Lloyd's opinion and do not recognize *P. tomentosus* in the American Flora. Furthermore, Overholts states that all American forms should be referred under the name *P. circinatus.* All three described the typical form as having straight setae because they have been led astray by the statement of Fries that the species was characterized by the homogeneous context of the fruiting bodies. Concerning *P. dualis* Pk., Shope considered it the same as *P. circinatus,* while Overholts gave a varietal rank because of the curved setae which in the typical form are straight. Lowe considered it a good species.

Jørstad and Juul (1938) worked out the taxonomy of the species with Norwegian material. They recognized two varieties to *P. tomentosus* Fr.: *P. tomentosus* var. *americanus* and *P. tomentosus* var. *circinatus.* They made the variety *americanus* because of Lloyd's statement (1912) that *P. tomentosus* Fr. does not exist in the American flora, but only a related form. The variety *circinatus* was suggested for *P. circinatus* Fr. because they said there is no definite line of demarcation between Fries' species. They make no mention of Sartory and Maire who made the same variety in 1922.

Haddow, in 1941, based all his discussion on specimens of the Curtis Herbarium identified and labelled by Fries himself. He recognized the duplex context for both *P. tomentosus* and *P. circinatus;* the former had straight setae and the latter curved ones. Haddow did not agree that the curved setae character was sufficient to make a new species as did Fries, thus he called it *P. tomentosus* var. *circinatus.*

As a resumé, the following table shows the real position of each specimen.

Author	*Polyporus tomentosus* Fr.	*Polyporus circinatus* Fr.
Fries (1851)	Polystictus tomentosus	———
Peck (1878)	———	P. dualis
Cooke (1886) "	Polystictus tomentosus	Polystictus circinatus
Saccardo (1888)	Polystictus tomentosus	Polystictus circinatus
Karsten (1889)	Onnia tomentosus	Onnia circinatus?
Ellis & Everhart (1889)	Mucronoporus tomentosus	Mucronoporus circinatus
Hennings (1898)	Polystictus tomentosus	Polystictus circinatus
Patouillard (1900)	Xanthochrous circinatus	———
Murrill (1904)	Coltricia tomentosa	Coltricia tomentosa
Lloyd (1908) (1912)	Polyporus tomentosus Polyporus circinatus	Polyporus dualis
Ames (1913)	Polystictus tomentosus	Polystictus circinatus
Neuman (1914)	———	Polyporus tomentosus Polyporus dualis

Author	*Polyporus tomentosus* Fr.	*Polyporus circinatus* Fr.
Bresadola (1920)	———	Polyporus dualis Polyporus triqueter
Sartory & Maire (1922)	Polyporus tomentosus	P. tomentosus var. circinatus
Konrad & Maublanc (1926)	———	Fomes (Xanthochrous) circinatus
Bourdot & Galzin (1927)	———	Polyporus circinatus
Killerman (1928)	Polystictus tomentosus	Polystictus circinatus var. triqueter
Shope (1931)	Polyporus circinatus Polyporus dualis	
Overholts (1933)	Polyporus circinatus	Polyporus circinatus var. dualis
Lowe (1934)	Polyporus circinatus	Polyporus dualis
Jørstad & Juul (1938)	Polyporus tomentosus P. tomentosus var. americanus	P. tomentosus var. circinatus
Haddow (1941)	Polyporus tomentosus	P. tomentosus var. circinatus

It is clear, from what has been written above, that the tangled taxonomy of the two types would not have resulted had it not been for Fries' early statement that *Polyporus tomentosus* possessed a homogeneous context, whereas a study of his specimens by the writer and others, has shown that the context of the sporophore is duplex in both types, the first of which should be recognized as *P. tomentosus* (with straight setae) and the second *P. circinatus* (with curved or straight setae in the same fructification). Assuming for the time being that the two species belong in the genus *Polyporus*, it appears to the writer that Fries was correct in making these separations, since, as it has been stated above, the two species are obviously different when seen together in the field (Plate I, fig. 1, 2). It is for this reason that the writer considers it desirable to follow Fries in recognizing these species as distinct rather than to follow Sartory and Maire, and Haddow in reducing *P. circinatus* to varietal rank under *P. tomentosus.*

The generic position of these two species would be greatly simplified if they were kept in the genus *Polyporus* as has been done by many, although Murrill (1916) and Donk (1933) and others have tended to divide the genus into smaller units and probably rightly so. On the basis of priority, Fries' genus *Polystictus* (1851) must be accepted for this and related species, since *P. tomentosus* was specifically mentioned as an example of the genus and therefore can be taken to represent the type of the genus. For this reason, it seems best to consider that *Polyporus tomentosus* and *Polyporus circinatus* should be known as *Polystictus tomentosus* (Fr.) Fr. and *Polystictus circinatus* (Fr.) Cke.

DISTRIBUTION

Since they have first been described by Fries, *P. tomentosus* and *P. circinatus* have been found abundantly in Asia, Europe and America.

Because frequently they have been misnamed, the writer has prepared from the literature a list of localities and has tried to indicate the distribution under *P. tomentosus* Fr. and *P. circinatus* Fr. Where there is any question of the accuracy of the determination, the author name is followed by a (?).

Locality	*Polystictus tomentosus* (Fr.) Fr.	*Polystictus circinatus* (Fr.) Cke.
Africa	Lloyd(?) (1920)	
Austria	Lloyd (1908)	
China		Teng (1932)
Canada		
Prince Ed. Is.	Ell. & Evh. (1889)	
Ontario	Lloyd (1908), Faull (1922)	
Manitoba & Saskatchewan	Bisby (1938)	
Nova Scotia	McKay(?) (1904, 1908)	Wehmeyer (1940)
New Brunswick	Hay (1903, 1905)	Hay (1903, 1905)
Germany	All. & Schn. (1886), Hennings (1898), Murrill (1904)	Hennings (1898) Murrill (1904)
Japan		Shirai(?) (1927
Sweden	Fries (1863), Lloyd (1908, 1912), Murrill (1904, 1908)	Fries (1863), Lloyd (1908), Murrill (1908)
United States		
California	Lloyd (1911, 1915)	Murrill (1915)
Colorado	Kauffman (1921), Lloyd (1908, 1916, 1920), Murrill (1904), Seaver & Shope (1936), Shope (1931)	
Dist. of Columbia	Lloyd (1922)	
Florida	Lloyd (1920)	
Idaho (northern)	Boyce (1938), Hubert (1929, 1931), Martin (1929)	Haskell & Wood(?) (1930), Hubert (1931)
Iowa	Wolf (1931)	
Maine	Lloyd (1923), Murrill (1904)	White(?) (1902), Ricker (?) (1902)
Maryland	Lloyd(?) (1908)	
Massachusetts	Lloyd (1907, 1908, 1911, 1912, 1913, 1914, 1915, 1921), Murrill (1904)	
Michigan	Kauffman (1911), Lloyd (1912), Longyear (1904), Overholts (1916), Povah (1935)	
Minnesota	Hubert (1924, 1931), Lloyd (1920, 1922) Martin (?) (1925)	Haskell & Wood (1930)
Montana	Hubert (1931)	
New Hampshire	Murrill (1904)	
New Jersey	Murrill (1904)	Ellis(?) (1890), Ell. & Everh.(?) (1889)
New York	Burnham & Latham (1914, 1924), Lloyd (1913, 1915, 1916, 1920, 1923), Murrill (1904), Peck (1869, 1880, 1893, 1899), Saccardo (1888)	Peck (1878, 1894)

Locality	*Polystictus tomentosus* (Fr.) Fr.	*Polystictus circinatus* (Fr.) Cke.
North Carolina	Curtis (1867), Lloyd (1914)	Atkinson & Schrenk(?) (1893)
Pennsylvania	Overholts (1933)	
Rhode Island	Bennett (1888)	
Tennessee (east)		Hesler (1929)
Vermont	Lloyd (1908, 1911, 1915), Murrill (1904)	
Washington	Hubert (1931), Lloyd (1916)	
West Virginia	Lloyd (1908, 1920), Murrill (1904)	
Wisconsin	Dodge (1914), Neuman (1914), Overholts (1916)	
Wyoming	Seaver & Shope (1935, 1936)	

To complete this list, the writer has plotted on a map the North American localities of the specimens of *P. circinatus* (Fr.) Cke. kept in the Farlow Herbarium. It seems that this species reaches its southern limit at the 36th parallel of latitude (Plate I, fig. 3). It is probably limited by the temperature and if so it could be expected farther south in the mountains.

History as a Parasite

Many writers have discussed the taxonomy of the two Friesian species since 1878, and still more mycologists have collected them in the forests, but very few, either in the Eastern or Western Hemisphere, have worked out the parasitism of these species.

In the Eastern Hemisphere, Jørstad and Juul (1938), after a discussion of the taxonomy of the species, questioned whether *P. tomentosus* Fr. has any parasitic tendencies and mentioned the fact that in Sweden it has been found on a root of spruce which did not present any rot. However, the ability of *P. circinatus* to cause rot is not doubtful and they gave the general characters of the rot as it occurs in Sweden and mentioned the similarity that this particular one has with that caused by *Fomes pini.*

The first in North America to report this species as a parasite was Dr. Faull (1922) who found that, in Ontario, it was causing a root- and butt-rot in spruce, hemlock and eastern white pine. Giving the description and habits of the sporophores, he identified them as being *P. tomentosus* Fr., but his herbarium specimens for that region show that *P. circinatus* Fr. was also abundant. He mentioned the fact that the infection was very much localized and further added that in the Otter District of Ontario a high percentage of white pine is affected.

Hubert (1931) reported that *P. circinatus* attacked roots and butt sections of western white pines in northern Idaho, but considered it to be a wound fungus and commonly associated with fire scars. He made a comparative study of *P. circinatus* and *Trametes Pini* and clearly described the similarities and differences between the two rots based on the macroscopic and microscopic characters of the two different decays, and the differences in the cultural characters of the two pathogens.

Christensen (1940) published a brief note on *P. circinatus*, giving the cultural characteristics and a description of the decay and of the sporophores and mentioning the importance of this disease in northern Minnesota as the cause of windthrow and premature death of the trees.

From this brief resumé of the literature it is apparent that although we have a certain body of facts in regard to the type of decay, the microscopical and macroscopical characters of the decayed wood, and of the cultural characters of the fungus, we have very little knowledge concerning the parasitic nature of the fungus, of geographical or other factors influencing infection, and little information about the biology of *Polystictus circinatus*. For these reasons and since the fungus seems to be of local importance because of its effect on the spruce forests of the Province of Quebec, the writer decided to make more intensive studies of the fungus in an endeavor to discover further facts bearing on the biology of the fungus and its relation to the host. At the same time, it was hoped to explain the relation of other butt-rot fungi to their hosts.

STUDIES ON THE HOST-PARASITE RELATIONS

Field Observations

In undertaking this study of *Polystictus circinatus*, an intensive survey was made to determine the occurrence of this species in the Province of Quebec, especially along the north shore of the St. Lawrence River and in the Gaspé Peninsula as well as in the Laurentide National Park area.

On the Gaspé Peninsula, and more especially along the northern side, the fungus appears to be of rather frequent occurrence, whereas on the south side it is somewhat scarcer. On the northern side of the Gaspé Peninsula in the vicinity of Mt. Albert, infection[2] was locally very high, (100%), in the York River area infection amounted to 95%, and at Lake Ste. Anne approximately 50%. On the north shore of the St. Lawrence River, near Lake Walker, the infection in the valley was about 20% and on the mountain slope up to 80–90%. On the other hand, in the Laurentide National Park, no evidence of infection could be discovered, even though that region is intermediate between Ontario, where Faull (1922) states that the fungus is very abundant, and the North Shore of the St. Lawrence.

The high degree of rotting of spruces by *Polystictus circinatus* indicates that this fungus may be of considerable importance in the Province of Quebec, and the gap in the distribution of the species represented by the complete or nearly complete absence of the fungus in the Laurentide National Park indicates that there may possibly be some ecological factor involved which not only would furnish information on the distribution of *P. circinatus* but might also help to explain host-parasite relations in the heavily rotted areas.

[2] As shown by the obvious symptoms of butt-rot at stump section.

For the understanding of the behavior of the disease, it would be of interest to know if this disease occurs on trees weakened by age, crowding, competition with other species, by storm or insect damages.

Christensen (1940), according to observations made in Minnesota, states that *P. circinatus* can infect trees as young as fifteen to twenty-five years old. From the writer's observations it can be stated that trees of forty years age presented visible decay at the stump section. Since they must have been infected earlier, it is probable that the age of infection given by Christensen is near the truth. According to the same observations, Christensen stated that "The fungus does not merely accompany stagnation and senescence but, if present at all, is likely to be one of the primary causes of such conditions." The writer agrees with Christensen that it sometimes happens that *P. circinatus* will kill the tree, but he does not think that it will always bring a premature senescence of the trees. From the data obtained from the Gaspé and North Shore regions, it is shown that the average age for the infected trees in Gaspé is 90 years, while it is 130 years for the North Shore region. The average age for sound trees is respectively 85 and 114 years. Thus, it seems significant that, on the whole, infection by *P. circinatus* appears to delay senescence.

The effect of crowding does not seem to have much influence on the occurrence of the disease. The disease was found where tree cover was very dense or loose, fruiting bodies having been found in places where the canopy was so dense that herbaceous plants could not grow, as well as in places where the canopy was sufficiently open to permit the growth of these covering plants. Hence, crowding is not a determining factor for the disease. Infection occurred either in pure stands of spruces or in mixed stands of spruce and fir. But in these mixed stands, infection has rarely been found when the percentage of firs was higher than 60%. This might be explained by the fact that the fir grows where soil is richer and where infection of spruce is relatively infrequent. Incidentally, *P. circinatus* was not found in stands of mixed soft and hardwoods, although *P. tomentosus* occurred in such stands. Again this may be explained by the fact that infection is less frequent in richer soils. Competition between host species does not seem to favor any tendency for infection. It can be stated, rather, that infection is most commonly found in pure stands where conditions for the growth of the trees are less favorable.

In the Gaspé region and on the north shore of the St. Lawrence River, observations were made on the occurrence of the butt-rot; there was no correlation between spruce sawfly epidemic, which was very severe, and the rotting of spruce by *P. circinatus*. At Mount Albert and at Lake Ste. Anne the black spruce was rotted, whether damaged or undamaged by the spruce sawfly, and the disease was found independently on both of them. Furthermore, in places like Petite Rivière-à-Marte and York River where there was up to 95% and 100% infection by the disease, the damage by the spruce sawfly was nonexistent. Except for the spruce sawfly epidemic

we have not seen, during our work, any sort of insect attack. It is therefore fairly evident that the rot caused by *P. circinatus* is not related to, or a result of, insect attacks.

Storms which break branches or make scars on the trunks of trees do not appear to have any influence on infection by *P. circinatus*, since infection takes place through underground parts. Nevertheless, a large number of forest soils in Quebec being thin, the rooting of trees is superficial and hence, under the action of the wind the trees oscillate and some small roots may break off and infection by *P. circinatus* may take place. Yet careful studies did not furnish evidence of increased infection. In addition, it may be remarked that in no case did entrance of the fungus into the wood take place through other parts than those underground, or which were at least in contact with the duff. Hubert (1931) states that this disease is often associated with fire scars but we believe that those scars had to be in contact with the ground. In places where infection was up to 85% and 100%, we have not seen a single case in which infection occurred at other places than those mentioned above. However, from inoculation experiments carried out in Duchesnay, it has been found that if the mycelium comes in contact with a scar on the trunk, it will invade the wood cells. Thus, it can be suspected that under natural conditions, the spores of the fungus must germinate in the humus.

In our North Shore experiments we have organized some kind of rudimentary meteorological stations in order to determine if temperatures, maximum and minimum, the quantity of rainfall, the relative humidity of the air, and the evaporation rate would be reflected in the number of infected and non-infected stands. The different measurements obtained at the two places had no significance, and none of the meteorological factors could be correlated with infection or non-infection of the stand.

As a rule we can state that the fungus invades very young trees and is seen in old ones, but the occurrence of this disease is not correlated with any crowding, competition or damage of any sort, or with local meteorological factors.

Effects of Temperature and Humidity on Sporophore Production

Bearing in mind that the practical aspect of the subject is the control of the disease, field observations were made to determine the factors bringing about the fructification of the fungus, since the control of a disease is sometimes attempted by the removal of the fruiting bodies.

During the summer of 1941, which the writer spent in Shelter Bay on the North Shore of the St. Lawrence River, it was only on the 15th of August that he found sporophores of *Polystictus circinatus*. As they are produced at about the same time of the year, he has tried to correlate the maximum and minimum temperature and the relative humidity of the air with the appearance of sporophores. For this purpose the following figures of temperature and humidity have been brought together in table I.

Table I

GIVING THE MAXIMUM AND MINIMUM TEMPERATURE AND THE RELATIVE HUMIDITY OF THE AIR IN SHELTER BAY, FROM JULY THE 15TH TO AUGUST THE 21ST 1941

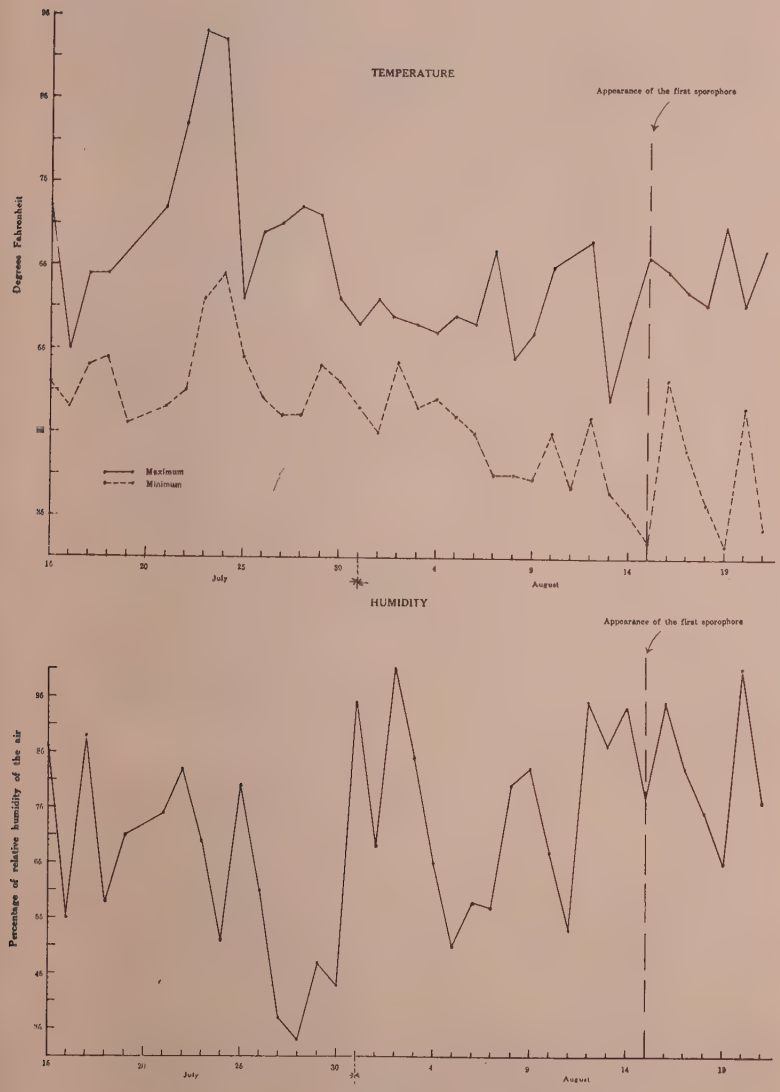
Date	Temperature Max.	Min.	Humidity	Date	Temperature Max.	Min.	Humidity
15 July	72.0	51.0	86	4 August	57.0	49.0	65
16 "	55.0	48.0	55	5 "	59.0	47.0	50
17 "	64.0	53.0	88	6 "	58.0	45.0	58
18 "	64.0	54.0	58	7 "	67.0	40.0	57
19 "		46.0	70	8 "	54.0	40.0	79
21 "	72.0	48.0	74	9 "	57.0	39.5	82
22 "	82.0	50.0	82	10 "	65.3	45.0	67
23 "	93.0	61.0	69	11 "		38.6	53
24 "	92.0	64.0	51	12 "	68.0	47.5	74
25 "	61.0	54.0	79	13 "	49.0	38.0	86
26 "	69.0	49.0	60	14 "	58.5	35.5	93
27 "	70.0	47.0	37	15 "	66.5	32.0	77
28 "	72.0	47.0	33	16 "	64.5	51.5	94
29 "	71.0	53.0	47	17 "	62.3	43.3	82
30 "	61.0	51.0	43	18 "	60.5	36.5	74
31 "	58.0	48.0	94	19 "	70.0	31.5	65
1 August	61.2	45.0	68	20 "	60.3	48.3	100
2 "	59.0	53.5	100	21 "	67.0	33.8	76
3 "	58.0	48.0	84				

It can be seen from the graphs of maximum and minimum temperatures (Graph 1) that the average of both has a tendency to be lower after the 15th of July. Also, it can be seen that the maximum temperature after the 30th of July averaged 60° F. and fell below 50° F. on the 15th of August. It seems that the 60° F. temperature is the critical one for initiating the fructification of *P. circinatus*. Since the figures given in Table I and in Graph 1 are for air temperature it should be pointed out that the temperature of the soil and of the tree would most likely be neither as low nor as high as the air temperature. Although those data have been taken only during one season and at one locality, they seem to indicate fairly well that when the average temperature of the day approaches the minimum temperature for mycelial growth, the vegetative phase is checked and the reproductive stage is initiated a short time before fruiting bodies actually appear.

Reference to Graph 2, presenting the percentage of relative humidity of the air against the time of the year make it evident that after the first day of August and up to the time fruiting bodies appeared, the percentage of relative humidity did not go below 50% and averaged 81.7%, while before that date, from the 15th of July up to August, the relative humidity was as low as 35% and averaged 64.3%. From the 15th of August up to

GRAPH 1. (Above) The relation of maximum and minimum temperatures to the appearance of sporophores.

GRAPH 2. (Below). The relation of atmospheric humidity to the appearance of sporophores.


TEMPERATURE
Appearance of the first sporophore
Degrees Fahrenheit
Maximum
Minimum
July
August
HUMIDITY
Appearance of the first sporophore
Percentage of relative humidity of the air
July
August

GRAPH 1, 2

September, the best time for sporophore production, the relative humidity was never lower than 65%, with an average of 85.7%. We have remarked that the sporophores come on trunks or roots always very close to the soil, a fact that substantiates the evidence tending to show that a relatively high humidity favors not only growth, but at a later date, when vegetative growth has been checked, also favors the production of fruiting bodies. Just how much the percentage of relative humidity becomes a limiting factor cannot be asserted from the data we have, but it is at least certain that an average of around 80% is favorable.

As far as light is concerned, it can be said that the sporophores are more generally found in diffused light. However, in one case, one was found exposed to the afternoon sunlight. From laboratory studies it has been found that the related *P. tomentosus* grows better in diffused than in bright light or in darkness.

Although not conclusive, these data furnish good indications that the appearance of the sporophores of *P. circinatus* is correlated principally with temperature and humidity and that the time of fruiting corresponds with the period when the low temperature checks vegetative growth and stimulates reproductive growth. This period also correlates with the time when the average relative humidity is on the increase and thus is furnished the water necessary to enable the fungus to complete the fruiting stage and to ripen the sporocarps. Exposure to light appears, if it is important at all, to play only a very secondary rôle in initiating the formation of the fruiting body. However, it is possible that once the fructifications are above the surface of the soil, light may have some influence on the formation of the hymenium and on the production of the spores. If this is so, since the fruiting bodies are produced mostly in the deep shade, it is evident that only very low intensities of light are needed to exert an influence on fructification.

EFFECTS ON HOST

In addition to some ecological data concerning the production of sporophores, field observations have also given some information concerning the effects of this disease on its host as, for instance, the external characters which diseased trees present and the kinds of breaking the rotted, fallen trees will present.

The writer has observed that in early stages of infection the trees do not present externally any signs of disease, but as the infection reaches an advanced stage, the foliage of the trees turns pale yellow-green. Another external character which sometimes accompanies the advanced stage of decay is the exudation of resin at the base of the trees. Although these characters are not specific to the infection by *P. circinatus*, they help to spot the disease in regions where it is known to occur. It has already been stated that field observations indicate that the infection of the host takes place through the lateral roots, as is shown by the fact that when subjected to strong winds the trees blow over very readily and in a char-

acteristic manner. By the comparison of trees infected by *P. circinatus* and of those attacked by *Poria subacida*, this point can easily be brought out. In this latter species, it was found that penetration was through the central or tap root and from there the rot progressed into the stump leaving the lateral roots unharmed; as a result the trees broke off about one to two feet above ground level. In *P. circinatus*, on the other hand, when the lateral roots have been weakened by decay the trees blew over and at the same time the tap roots were pulled from the ground. Further studies substantiate the above evidence. For example, at Shelter Bay in the valley level where both fungi occurred, the trees were blown over in a manner characteristic of trees infected by the two species of fungi. In this connection it should be pointed out that in the valley the soil is sufficiently deep so that the spruces develop both tap and lateral roots. On the mountain slopes however, where the rock is covered only by a layer of humus, and as a result tap roots are not developed, *Poria subacida* was absent and only *P. circinatus* was evident. Under such conditions as are present in the mountain habitat, only lateral roots could be infected. Thus there is furnished the added evidence that *P. circinatus* is confined to the lateral roots, at least during the early stages of growth.

GROWTH STUDIES

During the course of the studies in connection with penetration of the host by the fungus it became evident that it was desirable to make a comparative study of the growth of trees infected by *P. circinatus*[3] and non-infected ones, and at the same time to endeavor to discover the relations between the habitat and the infection of the trees as illustrated by their rate of growth. A survey was also made to find out whether or not there was any correlation between the age of the tree and the incidence of butt-rot. For this purpose studies were made in five localities, namely: the valley and mountain slope and summit in the vicinity of Lake Walker on the North Shore of the St. Lawrence River, and in the vicinity of York River and Lake Ste. Anne on the Gaspé Peninsula where ecological conditions seemed to be similar.

In these studies sections were made at D.B.H. of trees infected by *P. circinatus* and those not infected. In each type, the age of the tree was determined by a count of the annual rings and the diameter of the tree measured for each ten-year interval. The trees were segregated in age classes: (40–60) (70–90) (100–120) . . . etc. For each year class and for each locality the diameter of the average tree was calculated and from that the area of D.B.H. section was obtained for each ten-year interval.

[3] During the discussion on the growth rate of the trees, the terms "trees infected by *P. circinatus*" and "trees non-infected by *P. circinatus*" have been used having in mind the fact that the trees do or do not present visible signs of decay. It cannot be stated that trees which had no decay caused by *P. circinatus* were not in mycorrhizal-association with this fungus, nor can it be said that no other mycorrhizal fungus is present.

We assumed that the surface of the section of a conifer at breast height increased in proportion to the increase in volume of the tree. The growth rate was obtained by subtracting the logarithm of the surface of the section of two subsequent decades. Appendix I gives the area at D.B.H. section for each ten years and for each classification, Appendix II gives the corresponding growth-rate. In Graph 5, the rate of growth of infected and non-infected trees for the 130 150 year class have been plotted for different sites. From this graph it can be seen that in the York River and the Valley areas where the soils are favorable, the rate of growth of non-infected trees is greater than that of infected trees. Contrarily, on the East Slope and Mountain Top sites where the soil is shallow and leached and hence less favorable, the rate of growth of the infected trees is greater than those that are not infected. The significance of these facts will be discussed shortly. At this point it may be objected that there are not valid grounds for drawing any conclusions since the trees of each class may have encountered different ecological conditions during the different years of their growth. To answer this objection, the average rate of growth of trees for a given site and of infected and non-infected trees, together with the rate of growth of individual trees in each classification, was plotted by age (Graph 3) and by year (Graph 4). A comparison of these two graphs demonstrate that although there are minor differences, there is in general a very close agreement between the results derived by the two methods. Thus, whichever method is employed, the results are approximately the same and equally significant. For convenience and as a resumé of Appendix II, Table II has been prepared to show for each age class and for each region the percentage of number of decades in trees rotted by *P. circinatus* in which the rate of growth was higher than those not rotted by this particular fungus. Accompanying these percentages are symbols which indicate whether the area at D.B.H. section of the average tree rotted by *P. circinatus* is greater, equal, or smaller than that of the non-rotted trees.

Table II

	Gaspé Peninsula		Lake Walker Area		
Age class	L. Ste. Anne	York River	Valley	East Slope	Mountain Top
40–60	50% [ ]	0% −−		67% ++	
70–90	100% +	86% +		75% ++	29% [ ]
100–120	30% ++	70% −−	44% +	56% +	64% ++
130–150		42% −−	42% −	54% +	42% ++
160–180			38% −−	74% ++	
190–210			33% −−		
Average	62%	53%	38%	65%	47%

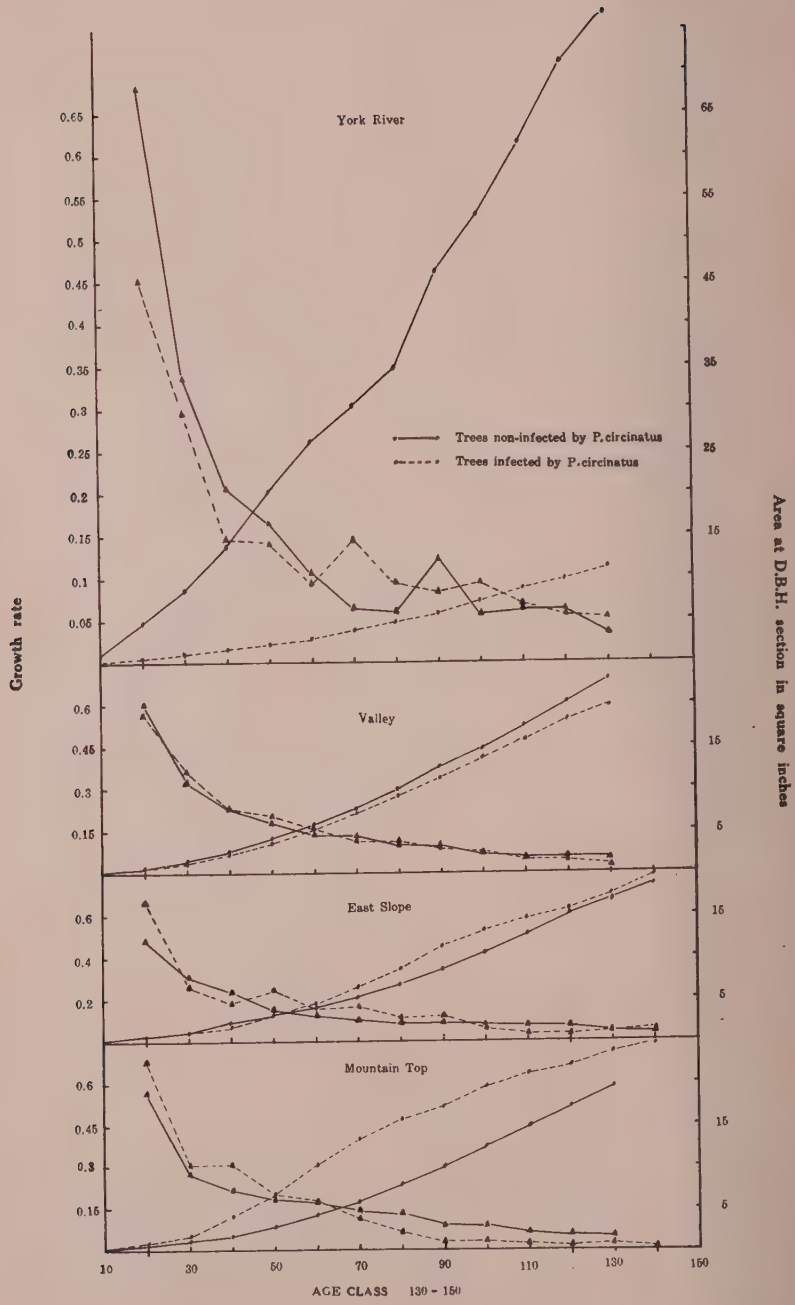
Area of rotted trees definitely higher ++, somewhat higher +, indifferent [ ], somewhat smaller −, definitely smaller −−.

GRAPH 3. The average rate of growth (heavy lines) and the growth of individual trees (light lines) of the 130–150 year class plotted by age.

GRAPH 4. The average rate of growth (heavy lines) and the growth of individual trees (light lines) of the 130–150 year class plotted by year.

GRAPH 4

GRAPH 3


York River
Trees non-infected by P.circinatus
Trees infected by P.circinatus
Valley
East Slope
Mountain Top
Growth rate
Area at D.B.H. section in square inches
AGE CLASS 130 - 150

GRAPH 5

Reference to Appendix I and Table II shows that in the two localities: York River and Valley, the area at D.B.H. section of the average rotted tree by *P. circinatus* is lower than that of the non-rotted trees except in age classes 70–90 and 100–120, but in all other localities the rotted trees have larger area at D.B.H. section than the non-rotted ones. Thus, it can be concluded that either the infection of the tree by this fungus is beneficial to the host or else that this fungus invades rapidly growing trees. This last hypothesis has to be discarded because the data from York River and Valley regions (Graph 5) show that the reverse is true. Examination of growth rates, Appendix II and Table II more especially, show that in all cases there always has been a period during the life of the tree when the growth-rate of trees infected by *P. circinatus* was higher than the non-infected ones, except for the age class 40–60 of York River. The percentages given in Table II show how long was this period. To explain why in York River and in the valley of the Lake Walker site, the area at D.B.H. section of trees infected by *P. circinatus* is smaller, it may be said that in these two regions the conditions for growth of the trees were not as poor as in the other regions, and that the growth of young non-rotted trees was at the beginning very good, while for some unknown reason it was somewhat delayed in the trees rotted by *P. circinatus*. Thus starting with a larger capital, the area at D.B.H. continued to be larger throughout the life of the tree even though the rate of growth was smaller during a few decades. On the other hand, in the other localities where the conditions of tree growth were poorer, the initial capital of the non-rotted trees was smaller or only slightly greater and was later exceeded by the faster growing but rotted trees.

In general it can be said that when there is little sub-soil, as under the conditions existing in the mountain slope and top, the trees show a larger diameter when rotted than when not rotted; on the contrary, when there is a considerable depth of sub-soil such as exists in the valleys, then the reverse holds true, but in all cases, with one exception, rotted trees always present a higher rate of growth, at least for a time, than do the non-rotted ones.

SOIL CONSTITUTION

Not having found any correlations between the occurrence of the disease and the state of crowding or competition between species, or the appearance of any insect epidemics, to explain the different relations between fungus and host in the various habitats, we have tried by soil analysis to correlate the occurrence of this disease with some salt deficiency. For this purpose we have used the method given by Hester, Blume and Shelton (1937) for rapid soil analysis. The results are shown in Appendix III which have been made to illustrate the effect of the concentration in the

GRAPH 5. The rate of growth and area at D.B.H. section of infected and non-infected tree at four different sites.

soil of phosphorus, CaO, NH_4, and potassium on the percentage of rotted trees in the stand. The conclusions are briefly summarized as follows:

1) — *Phosphorus:* From 0% to 30% infection, increasing concentration of phosphorus is correlated with increasing infection of the stand, but for higher infection than 30% no correlation can be made with the concentration of this element.

2) — *Calcium:* From 30% to 80% infection, increasing concentration of calcium seems to be correlated with increasing infection of the stand, but outside of these percentages of infection, nothing can be correlated.

3) — *Ammonium:* From 10% to 80% infection, increasing infection of the stand is fairly well correlated with increasing concentration of ammonium in the soil.

4) — *Potassium:* Up to 50% infection, decreasing potassium concentration in the soil accompanies increasing infection of the stand.

5) — *H-ion concentration:* In all the cases seen, infection was never found in stands where the humus had a greater H-ion concentration than pH 3.5. It seems that the average H-ion concentration has a tendency to be lower in stands with a higher percentage of infection, although this does not seem very specific. From culture studies, we know that this fungus can grow in artificial media having a pH between 3.5 and 8.6. The medium with a pH of 6.4 supported the fastest growth, but since there were not any cultures intermediate between pH 4.5 and pH 6.4, it cannot be stated that pH 6.4 is the optimum for growth of the fungus. Nevertheless, the optimum pH appears to be around pH 6.4. The pH of the humus of almost all infected stands are comprised between pH 3.58 and pH 4.40. Thus, we can state that generally the mycelium infects trees when conditions are not the optimum for the growth of the fungus, and accordingly the infection of trees could be interpreted as a reaction of the fungus against adverse conditions.

Thus, in so far as the percentage of rotted trees in the stand is not too high, the increasing degree of infection of the stand can be correlated with increasing concentration in the soil of phosphorus and ammonium, and decreasing concentration of potassium and calcium.

Now, instead of correlating singly the elements with the degree of infection of the stand, we will consider the elements by groups of two: phosphorus and calcium, ammonium and potassium.

1) — *Phosphorus and calcium:* It can be seen that, when infection is at or below 30%, the phosphorus concentration increases and calcium concentration decreases. From 30% to 50% infection, the phosphorous concentration decreases while calcium concentration increases. This goes on up to 70% infection. From that degree of infection up to 100%, calcium concentration will act in the same manner as phosphorus concentration.

2) — *Ammonium and potassium:* Ammonium and potassium concentrations always act in opposite ways, except between 0% and 10%, 50%

and 60% infection of the stand. So, it seems that as long as there are opposite (or mirror) correlations between phosphorus and calcium concentrations in the soil, the stand will have only weak infection. But as soon as these two elements correlate in the same sense, the stand is susceptible to a high degree of infection. In general, however, the correlation between ammonium and potassium does not seem so important.

NEEDLE ANALYSIS

According to experiments done at the Black Rock Forest, New York, the salt concentration in the leaves, or needles, is nearly proportional in pure culture to the concentration of these elements in the soil. So, to complete the information given by the soil analysis, we have analyzed needles of spruces from localities in which there were different degrees of rotting. The potassium, ammonium and phosphorus percentage of the dry weight increase in the needles with the increase of infection up to 30% (see Appendix IV). Even if in the soil the potassium concentration is low, the percentage of dry weight of this element in the needles is relatively high. It should be remarked also that the data in the three cases are about similar.

Although there are some indications from the soil analysis that increasing phosphorus and ammonium and decreasing potassium and calcium will favor rotting, those indications are valid only in the cases of low percentages of rotting. There must be some other factors which, in higher percentages, will govern the infection, but unfortunately we have not been able to determine such factors. Even the needle analysis does not give much information for greater rotting than 30%.

EVIDENCE OF SYMBIOTIC RELATIONSHIP

If soil and needle analysis do not give much information as to the factors determining the occurrence of rot, they do furnish good evidence that this parasitic fungus forms a symbiotic association with its host before becoming parasitic. The evidence is furnished by the fact that, as has just been pointed out above, under unfavorable conditions existing on the mountain top, rotted trees show greater growth than the non-rotted trees, whereas in the valleys where the essential nutrient elements have accumulated, the reverse is true and indicates that the symbiotic relationship is only effective when there is some mineral deficiency. The evidence is also furnished by the fact that infection takes place by the lateral roots and that sporophores of *P. circinatus* have been found associated with tree rootlets. The results of needle analysis also tend to show that there is a symbiotic relationship between the host and the fungus.

As stated previously, the introduction of the fungus into the host is made by way of the underground parts of the tree. Thus, the only possible way for the mycelium to penetrate the host will be either by underground scars, by direct penetration through the bark or symbiotic association with the tree. We have dug out about a dozen rotted trees in Ste.

Catherine and in Shelter Bay, and there are only a few cases where infection took place through scars on the roots. In all the other cases we could not find any particular place where the mycelium would have penetrated. Rather, we have seen the rot behaving exactly as a river. The main body of the river is the main lateral root and all or many of the secondary roots bring rot to the main lateral roots, and these meet in the trunk. Dr. Faull, in a personal communication, stated that he followed the rot up to the very tip of a root. The writer has made similar observations in Shelter Bay. Hence the mycelium must have penetrated directly through the bark or by symbiotic association. We do not have any evidence that it came through the bark, while we do have some for the symbiotic association hypothesis.

At least twice, sporophores of *P. circinatus* were found growing out of nests of rootlets. Hatch (1937) reported that sporophores coming out of rootlet-nests are quite frequent in the usual mycorrhizal fungi, and therefore since *P. circinatus* has twice been found connected with rootlet-nests, the evidence for its mycorrhizal relationships is further strengthened.

As has been previously stated, in the Gaspé and in the Lake Walker area the growth rate of rotted trees was higher than that of healthy ones. It is accepted that trees with mycorrhizae will have a larger rate of growth than those without, at least when the mycorrhizal relationship is efficient. On the other hand, we have seen that in the Valley (North Shore) of the St. Lawrence River and on York River (Gaspé), the diameter was smaller for rotted trees than for healthy ones. This has been correlated with the fact that in these two places the soil is richer in nutrient salts and better, apparently, for tree growth without the aid of *P. circinatus* as a partner, at least when it does not cause any rot.[4] We have seen also that the humus of these two places had less phosphorus than the others had. Rosendahl (1941) found that when the phosphorus concentration of soil was low, although mycorrhizal relationship was established, the intake of nitrogen and potassium was less than in similar seedlings grown with an adequate supply of phosphorus. Therefore if symbiotic relationship is to be of greatest benefit to the tree, then a suitable concentration of phosphorus is required.

TABLE III

THE CONCENTRATION OF THE VARIOUS MINERAL ELEMENTS IN THE SOIL IS GIVEN ACCORDING TO THE DIFFERENT LOCALITIES STUDIED

	pH		K		NH_4		P		CaO	
Locality	Inf	Non	Inf	Non	Inf	Non	Inf	Non	Inf	Non
Gaspé Peninsula										
Lake Ste. Anne	3.81	3.79	31	35	23	19	5.00	3.63	165	131
York River	3.80	3.74	39	35	26	24	*4.75*	6.50	97	260
L. Walker area										
Valley	3.74	4.07	20	22	20	22	*2.60*	12.50	80	40
Mountain Top	4.06	3.75	40	8	13	23	12.50	4.20	80	24
East Slope	3.95	3.95	5	23	15	32	12.50	10.25	40	48

[4] Refer to footnote page 537.

As seen from Table III the writer's observations substantiate this conclusion since in the valley of the Lake Walker area and York River area in Gaspé, the concentration of phosphorus was relatively low and this was correlated with a low percentage of length of time beneficial to rotted trees. It can be seen also that at Lake Ste. Anne where the concentration of phosphorus was not optimum, the infection in age class 100–120 was beneficial for only 30% of the time (Table II). The growth rates have been discussed in greater detail in a previous paragraph.

Another good character which seems to indicate the symbiotic relations of *P. circinatus* with the trees, is the salt content of the needles. Routien and Dawson (1943) suggest "that mycorrhizae increase the salt absorbing capacity of the roots . . . The increased salt uptake may then be reflected in a greater rate of growth." Finn (1942) stated: "It is seen that nitrogen and potassium were taken up in larger quantities by the inoculated seedlings than by the uninoculated ones. Phosphorus was absorbed in a slightly larger quantity by the inoculated seedlings than by the seedlings which were not inoculated." Thus, it is admitted now that plants with mycorrhizae will generally absorb more nitrogen, potassium and phosphorus than those without.

In order to check the mycorrhizal nature of *P. circinatus*, we have chemically analyzed spruce needles to find the percentage of these three elements in the needles both in rotted and non-rotted trees.

The needle analysis reveals that the phosphorus percentage in relation to the dry weight of the needles is lower for rotted trees than for healthy ones in the general average and in the data from York River, while it is higher at Lake Ste. Anne and at Chandler. Data from Finn (1942) reveal that the phosphorus intake by the mycorrhizal seedlings is higher than for the non-mycorrhizal ones, but the percentage to the dry weight is smaller even though the intake is larger. The difference, as shown by Finn, is 0.020% while the writer found a difference of only 0.011%. On York River this percentage is lower or only 0.007% while at Lake Ste. Anne it is higher or 0.049% and at Chandler 0.054%. This, however, has not definite significance because when there is a greater amount of phosphorus in the needles, there is a correspondingly greater concentration of this element in the soil. Thus, it cannot be unqualifiedly concluded that the infection by *P. circinatus* was beneficial to the trees although there seems to be evidence tending to indicate that such is the case.

As in the phosphorus relations, the percentage of nitrogen in the needles of rotted trees is higher, in the general average, than in the needles of healthy ones. Although the general average is higher for rotted trees than for healthy ones (Appendix VI), the percentage at Lake Ste. Anne and at York River are lower, respectively of 0.002% and 0.003%, although the soil analysis from these places (Appendix V) shows that soil under rotted stands had a higher concentration of ammonium salts than the healthy ones. Even if the nitrogen percentage of the needles is lower

(0.002%) for rotted trees than for healthy ones, this difference is so small that it probably is of little significance. However it is interesting to note that nitrogen concentration in the needles is higher for rotted trees than for healthy ones only when the concentration of nitrogen is lower in the soil. For example, at Lake Ste. Anne and on York River, the rotted stands had higher concentration of ammonium salt than the non-rotted ones and the reverse was true for the percentage of nitrogen in the needles. Exactly the contrary is found at Chandler. Nevertheless there seem to be indications that the infection by *P. circinatus* is sometimes beneficial to the host as a result of increasing the intake of nitrogen.

For the percentage of potassium in the needles, the analysis revealed that, in the general average, this percentage is lower for rotted trees than for non-rotted ones; however in the rotted trees of Lake Ste. Anne and of Chandler this percentage is much higher. This low percentage in rotted trees seems to be prevalent almost exclusively at York River. At that place we have found percentages as low as 0.062, 0.071, 0.085, and 0.094. In none of the other places were percentages found as low as these, and it was remarked that these low percentages came with heavily rotted trees. In Gaspé only 22% of the infected trees were rotted as high as D.B.H. section, but of the trees which have a low percentage of potassium 60% were rotted up to the D.B.H. section. In general the potassium percentage of the needles is low in all rotted trees of York River, 0.236% compared with 0.372% at Chandler and 0.418% at Lake Ste. Anne. This excessively low average might perhaps be explained by the fact that 88% of the most heavily rotted trees were from York River region. It can be seen from soil analysis that, at Lake Ste. Anne, although the concentration of potassium in the soil was smaller for infected stands than for healthy ones, the percentage of this element in the needles was greater. It is logical to suppose that the infection, at least at Lake Ste. Anne, has been beneficial to the trees for larger intake of potassium.

Thus if the data from York River region are excepted, we can state that the infection of the trees with *P. circinatus* has increased the intake of mineral salts. This beneficial effect should not be interpreted too categorically, but rather as a probability. It should be remembered also that the needles analyzed might, in many instances, have come from trees in which the parasitic have exceeded the beneficial effects of the previous symbiotic association. This would have lowered the average percentage for the rotted trees and might explain why, in the York River region where the trees are more heavily rotted than in the other regions, the percentages of all elements are so low.

The field observations, in addition to some facts concerning the behavior of the disease caused by *P. circinatus*, has brought out facts which seem to indicate fairly well that this fungus penetrates into its host by symbiotic association. Each fact in itself is not very conclusive but they all substantiate the same conclusion.

EFFECTS OF SEEDLING INOCULATION WITH P. CIRCINATUS

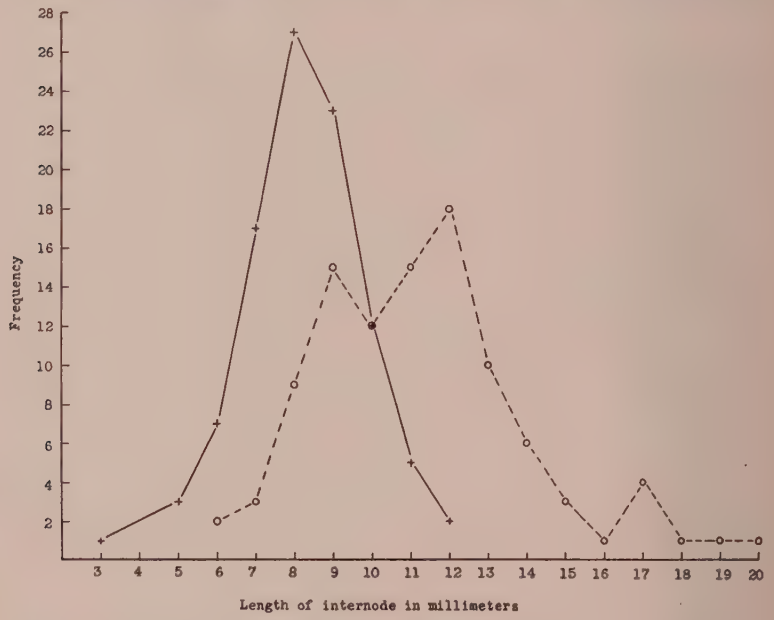
Having in mind all the evidence from field observations that *P. circinatus* was penetrating into the host through symbiotic association, the writer has tried to establish the mycorrhizal relationship between spruce seedlings and the fungus under laboratory control.

First, we have tried to culture seedlings under aseptic conditions with the Hatch culture chambers, but the experiment did not succeed. Later, loamy-clay soil was obtained from Saskatchewan where no trees are growing, and consequently in which there are no mycorrhizae forming fungi. This was suggested by the experiments done by Hatch (1937). After having sterilized and stratified spruce seeds, they were put in the ice box for two weeks in order to obtain a better germination. The loamy-clay soil was placed in wooden boxes previously sterilized and the seeds were sown. After germination in July, 1942, the seedlings grew in a greenhouse until January, 1943, when they were placed under the snow to allow a dormant period. At the beginning of April, 1943, they were dug out of the snow and put in the cold room (33° F.) for fifteen days to make the transition between the temperatures of the snow cover and the greenhouse less abrupt. After two weeks in the greenhouse, when the buds were bursting, half of the seedlings were inoculated on May 1, 1943, with cultures of *P. circinatus*, while the other half was reserved to serve as a check, although maintained under the same growing conditions. After three months of growth, namely on August 31, the seedlings from both series were removed and studied to determine what difference existed. It was immediately obvious (Plate II) that the inoculated seedlings had not only made a greater growth but that the needles were of a deeper green color and that the primary roots had produced more secondary roots.

To determine the relative growth of the inoculated seedlings and those not inoculated, they were measured from the primary node to the apex. The results of these measurements are presented in Graph 6 in which the actual figures are represented by crosses for the non-inoculated seedlings and circles for the inoculated ones. These figures are based on the measurements of a hundred seedlings for each series. It is immediately obvious that the non-infected seedlings show a fairly definite curve, whereas the inoculated ones follow essentially the same curve, although there is some deviation from the curve presented by the non-inoculated seedlings. This deviation, it seems, may be explained by the fact that the period of growth after inoculation was so short that complete mycorrhizal relationship had not yet become established. Despite this erratic behavior, however, it is quite obvious that even in so short a time as three months, the fungus did stimulate the growth of the spruce seedlings.

A further examination of the seedlings shows that while the roots of the uninoculated ones are not infrequently longer than the inoculated ones, nevertheless the latter were characterized by the production of a greater number of secondary rootlets which were frequently branched. In the

uninoculated plants these secondary rootlets, comparatively speaking, were very rarely branched. Thus, it can be seen that the fungus in this instance has added to the efficiency of the root system for absorption. This becomes all the more evident when it is seen that, despite shorter roots with increased secondary rootlets, the secondary internode of the stem of the inoculated seedlings, on the basis of ten specimens taken at random, totaled to 142.5 mm. whereas in the non-inoculated seedlings that were measured in the same way, the total was 113 mm. Furthermore, the



GRAPH 6. The relative rate of growth of inoculated (0) and non-inoculated (+) seedlings.

inoculated seedlings bore 727 needles and the uninoculated 548 needles, or respectively 51 and 48.5 needles per cm. of internode.

In addition to these obvious differences between the two series, there is the further difference that is furnished by the darker color of the needles of infected seedlings. The needles of non-inoculated seedlings in contrast to those inoculated were mostly yellowish green and in addition show the presence of anthocyanins, an indication, according to Mitchell (1934), that there is a phosphorus deficiency in the soil. Since the inoculated trees did not show this symptom of deficiency, it seems likely that the fungal symbiont helped to make available a larger phosphorus supply. Unfortunately the information is not available to enable us to make any statement as to how the process takes place.

The obvious differences observed in the size of inoculated and uninoculated seedlings, and the greater number of needles per centimeter of internode for the inoculated than for the uninoculated seedlings, led us to examine the microscopical characters of rootlets of the inoculated ones. Rootlets which we considered as having mycorrhizal relationship on account of their larger size were killed and imbedded in paraffin. It can be seen from the sections that the mycorrhizal relationship is of the regular type. The Hartig net is two to three cells deep, without apparent intracellular invasion. The mantle is homogenous (Plate III, fig. 1) and somewhat parenchymatous in structure, about three to four cells deep, with a smooth margin from which arise very few hyphae which penetrate into the surrounding cells. Sections made of rootlets found in a rootlet nest (Plate III, fig. 2) under a sporophore of *P. circinatus* show essentially the same type of mycorrhizal relationship. The mantle is homogenous, although thicker, parenchymatous in structure, with a smooth margin. The tannin layer is not very apparent, and locally seems to be two cells thick. The Hartig net is not so thick as the type we obtained by inoculation, but essentially the same type of mycorrhizal relationship is evident in the artificially and the naturally invaded rootlets. Thus, although the experiment was not done under aseptic conditions, it seems very probable that the endophyte here concerned is *P. circinatus*.

When all characters are taken into consideration, it seems safe to conclude that the fungus has a beneficial effect on its phanerogamic partner, at least in the early stages. Also these experimental results tend to substantiate the conclusions already drawn from field observations.

The observations that we have made so far, either on growth rates or on soil or needles analysis, seem to indicate that the infection of the trees by *P. circinatus* behaves as if the fungus was mycorrhizal. However, in our northern forests where the pH of the soil is relatively high and where nitrogen is chiefly supplied as ammonium salt, it would seem that the trees must be in mycorrhizal association to live under such conditions. We have seen that trees infected with *P. circinatus* behave, in comparison with trees not infected by this species, much in the same manner as trees that are in association with known mycorrhizal fungi. This relation between the fungus and the tree exists until some unfavorable factor, as yet unknown, upsets the balance between the symbionts. When this happens, then it would seem that the fungus readily becomes parasitic, and the mycelium, instead of remaining intercellular, as in the Hartig net, penetrates into the cells (Plate III, fig. 3) and travels backward along the rootlets, killing them as it proceeds. This would then explain the reason why the butt-rot seems to have its inception in the lateral roots rather than through wounds or through the tap root. In *Polystictus circinatus*, then, we have a butt-rot fungus that in the earlier stages of the development of the trees, instead of being a parasite, actually is beneficial until the host reaches a certain age, which might indicate senescence, the age being determined by local ecological conditions.

SUMMARY

The white pocket butt-rot of conifers caused by *Polystictus circinatus* (Fr.) Cke. has been studied because of its local importance in the Province of Quebec and because of its peculiar behavior.

Field observations have been made to correlate the occurrence of this disease with some ecological factors. The disease was localized in such definite loci of infection that it was thought that it was tied up with conditions of temperature, insect epidemics, mechanical damage, or with the chemical nature of the soil. However, none of those factors appeared to be responsible for the occurrence of the disease.

At the same time as the ecological factors were discarded as having no correlation with the disease, the field observations brought up evidence that this disease penetrated into its host by mycorrhizal association. Although none of the facts furnished any conclusive evidence, they all substantiate the same conclusion.

To bring more evidence, the writer has tried to establish mycorrhizal relationship between spruce seedlings and the fungus. The results indicate that the fungus has really formed a mycorrhizal association of the usual type.

If *P. circinatus* penetrates into its host through symbiotic association. and there is presumptive evidence that such is the case, this fact will open an entire new field in forest pathology. It will associate the two concepts of symbiotism and parasitism which were previously separated by air-tight walls. Those who are specifically interested in symbiotic problems will have to consider the pathological aspect of the question and the forest pathologists will have to be better acquainted with symbiotism in order to deal correctly with certain of their problems. Foresters will no longer be able to consider the butt-rots only as a reducing factor for the volume of the tree but will have to determine under which conditions the damage from parasitism exceeds the beneficial effects of symbiotism on trees, if it is demonstrated later, as it is not at all illogical to suppose, that butt-rotting fungi penetrate into the host by mycorrhizal relationship. These fungi in the Province of Quebec are all quite abundant; before trying to eliminate them by short cycle rotations, it will be necessary to know what part they are playing in the biological complex of our forest soil. Future researches will have to determine under which conditions parasitism follows the symbiotic association.

This field is new and wide open. It will certainly be of considerable interest to those who will have the advantage of working on such problems, and it promises to be at the same time of practical interest to foresters.

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Appendix I

AREA OF D.B.H. SECTION FOR EACH AGE CLASS

DATA FROM YORK RIVER, GASPÉ

Age Class: (40–60)		(70–90)		(100–120)		(130–150)	
Number of trees: (1)	(6)	(13)	(19)	(25)	(24)	(2)	(4)
A	B	A	B	A	B	A	B
1.34	1.27	1.34	0.61	1.09	0.58	1.03	0.21
5.35	4.13	4.48	2.41	3.06	1.61	4.97	0.58
20.37	8.44	7.96	5.48	5.88	2.77	8.61	1.15
32.15	13.24	11.08	9.45	7.33	4.01	13.87	1.61
40.65	16.73	14.29	14.08	9.80	5.62	20.39	2.24
58.67	23.00	17.90	17.91	11.65	7.34	26.10	2.77
		21.40	22.20	13.87	9.10	30.30	3.90
		22.20	26.36	16.05	11.08	34.80	4.84
		26.36		18.38	13.04	46.20	5.89
				20.89	14.72	53.00	7.33
				25.20	17.91	61.50	8.61
					19.62	71.15	9.81
						77.00	11.08

DATA FROM LAKE STE. ANNE, GASPÉ

Age Class: (40–60)		(70–90)		(100–120)	
Number of trees: (7)	(3)	(23)	(9)	(4)	(3)
A	B	A	B	A	B
0.54	0.67	0.39	0.26	0.12	0.39
1.76	1.91	1.47	1.21	0.50	1.34
3.26	3.57	2.96	2.96	1.03	2.77
5.09	5.88	5.22	5.62	1.99	5.35
7.18	7.64	7.64	8.44	2.96	8.44
7.80		10.15	12.43	4.72	12.04
		12.84	16.27	6.88	16.27
		13.87	18.63	9.28	21.14
			19.87	12.24	27.80
				14.08	32.80
				19.62	42.10
					44.30

A—Trees not infected (see footnote page 537).
B—Trees infected with *P. circinatus*.

Appendix I (continued)

DATA FROM THE VALLEY, LAKE WALKER AREA

Age Class: (100–120)		(130–150)		(160–180)		(190–210)	
Number of trees: (44)	(5)	(45)	(23)	(7)	(9)	(2)	(3)
A	B	A	B	A	B	A	B
0.20	0.32	0.18	0.16	0.23	0.04	0.10	0.01
0.67	1.15	0.72	0.58	0.98	0.11	0.29	0.04
1.40	2.68	1.54	1.34	2.24	0.26	0.54	0.06
2.50	5.09	2.68	2.32	4.36	0.42	1.15	0.13
3.90	7.80	4.12	3.68	7.18	0.67	1.99	0.26
5.48	10.71	5.75	5.36	11.27	1.03	3.36	0.39
8.12	13.04	7.80	7.03	16.05	1.47	4.36	0.62
10.53	15.82	9.98	9.10	21.14	1.99	6.02	0.82
12.84	20.12	12.64	11.46	26.65	2.59	7.18	1.09
16.73	20.88	14.93	13.66	32.15	3.36	9.10	1.40
	22.73	17.44	15.82	37.13	4.12	11.65	1.76
		20.12	18.15	43.21	5.22	13.87	2.23
		23.00	19.87	49.72	6.02	16.97	2.59
				55.45	6.88	20.37	3.06
				60.61	7.64	23.81	3.46
				67.38		26.92	3.79
						30.25	4.24
						33.78	4.36
						37.83	4.60

DATA FROM THE EAST SLOPE, LAKE WALKER AREA

Age Class: (40–60)		(70–90)		(100–120)		(130–150)		(160–180)	
Number of trees: (9)	(1)	(10)	(2)	(11)	(6)	(5)	(1)	(1)	(1)
A	B	A	B	A	B	A	B	A	B
0.42	0.77	0.16	0.18	0.20	0.18	0.20	0.13	0.13	0.13
2.41	1.99	0.42	0.46	0.67	0.72	0.62	0.62	0.39	0.50
3.06	4.12	1.03	1.15	1.40	1.48	1.27	1.15	0.77	1.15
5.09	8.12	1.68	1.91	2.15	2.50	2.24	1.76	1.34	2.24
7.18		2.77	3.36	3.26	4.12	3.16	3.16	1.76	3.79
		4.24	4.97	4.60	6.30	4.24	4.48	2.24	5.35
		5.62	7.68	5.48	8.44	5.48	6.59	2.87	7.49
		6.88	10.34	7.96	10.71	6.88	8.61	3.47	9.63
		7.96	15.82	9.98	13.04	8.61	11.46	4.48	12.64
				12.04	15.16	10.53	13.24	5.35	14.50
						12.64	14.50	6.16	16.73
						15.16	15.82	7.03	19.62
						16.97	17.44	8.61	22.19
						18.63	19.62	9.63	24.65
								10.16	26.36
								11.46	28.79

A—Trees not infected.
B—Trees infected with *P. circinatus*.

Appendix I (concluded)

DATA FROM THE MOUNTAIN TOP, LAKE WALKER AREA

Age Class: (70–90)		(100–120)		(130–150)	
Number of the trees: (21)	(3)	(31)	(1)	(13)	(1)
A	B	A	B	A	B
0.18	0.20	0.16	0.13	0.16	0.20
0.67	0.58	0.58	0.39	0.58	0.98
1.47	1.76	1.21	0.50	1.09	1.99
2.32	2.67	2.32	2.87	1.83	4.12
3.79	4.13	3.26	4.48	2.87	6.59
5.48	6.16	4.84	7.03	4.24	10.16
7.64	7.64	7.03	10.16	5.89	13.24
10.55	10.16	9.09	14.29	7.96	15.82
14.50		11.27	17.44	9.98	17.44
		12.74	20.37	12.43	19.62
		15.16	23.81	14.72	21.14
		15.37	25.79	17.20	22.19
				19.62	23.81
					24.65

Appendix II

GROWTH RATE BY AGE CLASSES

DATA FROM YORK RIVER, GASPÉ

Age Class: (40–60)		(70–90)		(100–120)		(130–150)	
Number of trees: (1)	(1)	(13)	(19)	(25)	(24)	(2)	(4)
A	B	A	B	A	B	A	B
0.6020	0.5104	0.5246	0.5864	0.4484	0.4436	0.6826	0.4520
0.5806	0.3110	0.2498	0.3574	0.2842	0.2354	0.3388	0.2960
0.1982	0.1956	0.1438	0.2366	0.0956	0.1608	0.2072	0.1468
0.1018	0.1016	0.1104	0.1730	0.1260	0.1460	0.1670	0.1422
0.1594	0.1380	0.0980	0.1044	0.0750	0.1160	0.1072	0.0932
		0.0774	0.0932	0.0756	0.0934	0.0646	0.1484
		0.0158	0.0748	0.0634	0.0858	0.0602	0.0940
		0.0748		0.0590	0.0706	0.1238	0.0848
				0.0554	0.0526	0.0592	0.0956
				0.0818	0.0852	0.0648	0.0694
					0.0396	0.0634	0.0566
						0.0342	0.0532

A—Trees not infected (See footnote page 537).
B—Trees infected with *P. circinatus*.

Appendix II (continued)

DATA FROM LAKE STE. ANNE, GASPÉ

Age Class: (40–60)		(70–90)		(100–120)	
Number of trees: (7)	(3)	(23)	(9)	(4)	(3)
A	B	A	B	A	B
0.5142	0.4556	0.5822	0.6716	0.6374	0.5408
0.2682	0.2718	0.3036	0.3884	0.6168	0.3162
0.1938	0.2168	0.2464	0.2780	0.2854	0.2858
0.1492	0.1134	0.1654	0.1770	0.1726	0.1980
0.0358		0.1238	0.1682	0.2024	0.1542
		0.1014	0.1168	0.1640	0.1308
		0.0336	0.0588	0.1298	0.1138
			0.0180	0.1200	0.1192
				0.0610	0.0714
				0.1440	0.1084
					0.0224

DATA FROM THE VALLEY, LAKE WALKER AREA

Age Class: (100–120)		(130–150)		(160–180)		(190–210)	
Number of trees: (44)	(5)	(45)	(23)	(7)	(9)	(2)	(3)
A	B	A	B	A	B	A	B
0.5166	0.5576	0.6020	0.5706	0.6274	0.4682	0.4748	0.4860
0.3216	0.3672	0.3328	0.3628	0.3604	0.3522	0.2724	0.2182
0.2500	0.2794	0.2398	0.2392	0.2898	0.2128	0.3296	0.3204
0.1938	0.1850	0.1878	0.2002	0.2170	0.2014	0.2384	0.2818
0.1480	0.1378	0.1442	0.1636	0.1956	0.1878	0.2278	0.1742
0.1704	0.0854	0.1324	0.1176	0.1536	0.1544	0.1126	0.2096
0.1128	0.0840	0.1072	0.1118	0.1198	0.1310	0.1406	0.1158
0.0862	0.1044	0.1024	0.1004	0.1006	0.1140	0.0774	0.1262
0.1152	0.0162	0.0726	0.0762	0.0814	0.0888	0.1026	0.1100
	0.0368	0.0672	0.0638	0.0626	0.1024	0.1076	0.0978
		0.0622	0.0596	0.0658	0.0620	0.0756	0.1044
		0.0580	0.0394	0.0610	0.0580	0.0876	0.0632
				0.0474	0.0454	0.0794	0.0730
				0.0386		0.0678	0.0542
				0.0460		0.0536	0.0386
						0.0504	0.0490
						0.0478	0.0118
						0.0492	0.0232

A—Trees not infected.
B—Trees infected with *P. circinatus*.

Appendix II (concluded)

DATA FROM THE EAST SLOPE, LAKE WALKER AREA

Age Class: (40–60)		(70–90)		(100–120)		(130–150)		(160–180)	
Number of trees: (9)	(1)	(10)	(2)	(11)	(6)	(5)	(1)	(1)	(1)
A	B	A	B	A	B	A	B	A	B
0.7574	0.4152	0.4312	0.4082	0.5166	0.6020	0.4862	0.6666	0.4570	0.5682
0.1040	0.3166	0.3892	0.3992	0.3216	0.3128	0.3098	0.2652	0.2980	0.3638
0.2214	0.2940	0.2130	0.2208	0.1856	0.2284	0.2444	0.1846	0.2428	0.2890
0.1492		0.2162	0.2454	0.1804	0.2182	0.1500	0.2544	0.1186	0.2290
		0.1848	0.1694	0.1592	0.1842	0.1280	0.1516	0.1044	0.1500
		0.1220	0.1894	0.0766	0.1268	0.1116	0.1678	0.1178	0.1460
		0.0884	0.1292	0.1618	0.1034	0.0968	0.1160	0.0826	0.1092
		0.0630	0.1846	0.0984	0.0854	0.0970	0.1244	0.1112	0.1180
				0.0814	0.0654	0.0874	0.0628	0.0774	0.0598
						0.0794	0.0394	0.0614	0.0622
						0.0790	0.0378	0.0572	0.0690
						0.0490	0.0422	0.0878	0.0536
						0.0405	0.0512	0.0488	0.0456
								0.0234	0.0292
								0.0522	0.0282

DATA FROM THE MOUNTAIN TOP, LAKE WALKER AREA

Age Class: (70–90)		(100–120)		(130–150)	
Number of the trees: (20)	(3)	(31)	(1)	(13)	(1)
A	B	A	B	A	B
0.5726	0.4546	0.5706	0.4560	0.5706	0.6800
0.3422	0.4814	0.3194	0.1110	0.2736	0.3098
0.1978	0.1826	0.2826	0.7606	0.2260	0.3166
0.2128	0.1878	0.1476	0.1938	0.1940	0.2034
0.1608	0.1744	0.1718	0.1960	0.1702	0.1882
0.1442	0.0934	0.1620	0.1600	0.1424	0.1150
0.1390	0.1238	0.1118	0.1480	0.1310	0.0772
0.1392		0.0930	0.0864	0.0984	0.0422
		0.0634	0.0676	0.0954	0.0512
		0.0654	0.0678	0.0732	0.0326
		0.0062	0.0346	0.0676	0.0210
				0.0572	0.0306
					0.0150

A—Trees not infected.
B—Trees infected with *P. circinatus*.

Appendix III

CONCENTRATION IN P.P.M. OF PHOSPHORUS, POTASSIUM, CALCIUM AND AMMONIUM AND H-ION CONCENTRATION OF THE HUMUS OF STANDS OF VARIOUS DEGREES OF ROTTING

Percentage of rotted trees in the stand	Phosphorus	Potassium	Calcium	Ammonium	P.H.
0%	5.17 (3.82)*	35 (10)	154 (104)	33 (13)	3.83 (0.29)
5%	6.87 (4.06)	47 (5)	110 (78)	23 (2)	3.58 (0.06)
10%	6.25 (3.64)	39 (4)	300 (50)	19 (5)	4.22 (0.5)
15%	5.0	40	165 (69)	20	3.70
20%	8.55 (3.33)	35 (5)	272 (78)	21 (4)	4.37 (0.03)
30%	10.00 (3.54)	33 (6)	53 (38)	24 (5)	3.72 (0.09)
50%	5.09 (3.45)	34 (14)	222 (99)	26 (2)	4.20 (0.37)
60%	7.81 (3.98)	40 (8)	111 (67)	27 (10)	3.76 (0.25)
70%	4.38 (0.63)	47 (5)	53 (19)	25 (5)	3.92 (0.06)
80%	8.75 (3.57)	42 (24)	300 (41)	30 (7)	4.27 (0.20)
90%	3.82 (0.82)	33 (12)	93 (67)	26 (8)	3.76 (0.16)
95%	8.75 (4.61)	40 (10)	165 (85)	27 (3)	3.93 (0.25)
100%	2.17 (2.05)	32 (13)	300 (50)	23 (7)	5.38 (1.02)

* Standard deviation.

Appendix IV

PERCENTAGE OF THE DRY WEIGHT OF THE NEEDLES OF PHOSPHORUS, POTASSIUM AND NITROGEN

Percentage of rotted trees in the stand	Phosphorus	Potassium	Nitrogen
0%	0.188% (0.055)*	0.339% (0.70)	0.658% (0.062)
5%	0.146% (0.032)	0.277% (0.053)	0.602% (0.051)
10%	0.143% (0.027)	0.278% (0.060)	0.664% (0.042)
15%			
20%	0.157% (0.042)	0.404% (0.082)	0.404% (0.082)
30%	0.194% (0.017)	0.545% (0.091)	0.744%
50%	0.184% (0.028)	0.306% (0.034)	0.631% (0.062)
60%	0.166% (0.030)	0.216% (0.070)	0.620% (0.051)
70%	0.148%	0.198%	0.626%
80%			
90%	0.148% (0.029)	0.232% (0.135)	0.652% (0.093)
95%	0.182% (0.007)	0.264% (0.115)	0.661% (0.061)
100%	0.153% (0.028)	0.294% (0.038)	0.781%

* Standard deviation.

Appendix V

THE pH AND THE CONCENTRATION OF K, NH_4, P, CaO IN THE SOIL OF THE VARIOUS LOCALITIES STUDIED

Locality	pH		K		NH_4		P		CaO	
	Inf	Non	Inf	Non	Inf	Non	Inf	Non	Inf	Non
Gaspé Peninsula										
Gaspé Park	4.95	3.81	41	38	20	21	2.75	4.13	290	72
Lake Ste. Anne	3.81	3.79	31	35	23	19	5.00	3.63	165	131
Chandler	4.24	4.01	37	32	22	28	5.75	4.13	260	216
York River	3.80	3.74	39	35	26	24	4.75	6.50	97	260
Petit Pabos River	4.60	4.65	43	40	19	25	5.00	12.50	300	250
West Branch Pabos River		3.81		31		26		3.63		182
Pecan River	4.06	3.90	34	25	25	30	4.88	3.13	250	250
Four Lakes (Marsoui)		3.85		25		25		12.50		40
Petite Rivière-à-Marthe	4.30	3.85	50	35	17	17	5.00	4.38	250	80
North Side Mt. Albert	6.45	3.90	20	50	30	30	0.75	3.75	350	40
Lac des Américains Trail	5.15	4.20	48	40	20	23	1.25	3.75	350	250
East Side Mt. Albert	6.45	3.90	20	50	30	30	0.75	3.75	350	40
Lake Walker Area										
Valley	3.74	4.07	20	22	20	22	3.23	12.50	80	40
Mountain Top	4.06	3.75	40	8	13	23	12.50	4.13	80	24
East Slope	3.95	3.93	5	23	15	32	12.50	10.25	40	48
Philibert Slope	3.81		30		18		8.75		56.	

Appendix VI

PER CENT OF DRY WEIGHT OF THE MINERAL ELEMENTS IN THE NEEDLES FROM THE DIFFERENT LOCALITIES STUDIED

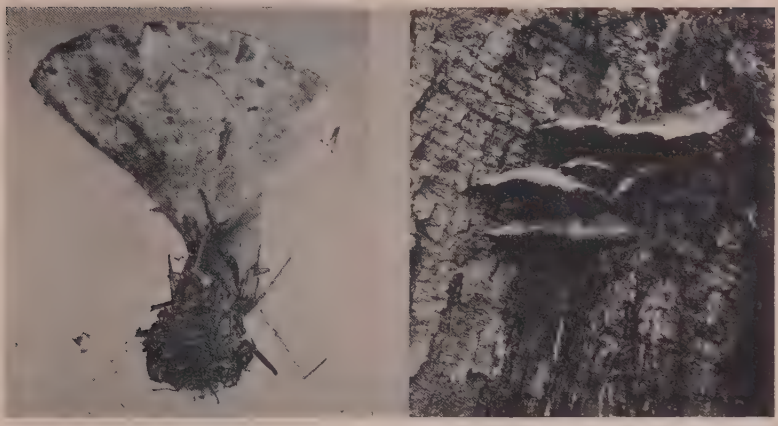
Locality	Phosphorus		Potassium		Nitrogen	
	Inf	Non	Inf	Non	Inf	Non
Gaspé Park	0.143%		0.271%		0.765%	
Lake Ste. Anne	0.224%	0.175%	0.418%	0.298%	0.671%	0.673%
Chandler	0.169%	0.115%	0.372%	0.344%	0.650%	0.622%
York River	0.164%	0.171%	0.236%	0.351%	0.631%	0.634%
General Average	0.164%	0.175%	0.264%	0.317%	0.654%	0.615%

EXPLANATION OF PLATE I

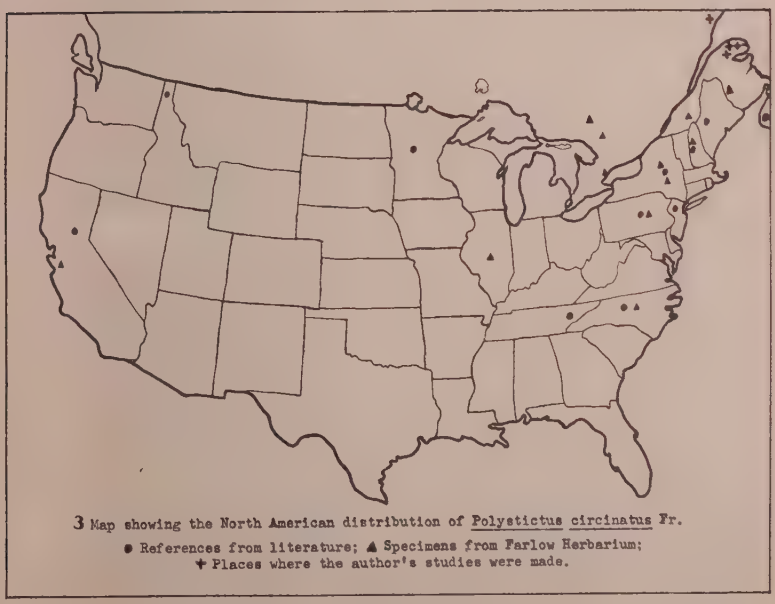
Fig. 1. *Polystictus tomentosus* (Fr.) Fr. Side-view to show the distinct stipe which is nearly central.

Fig. 2. *Polystictus circinatus* (Fr.) Cke. Side-view to illustrate the sessile, applanate fruiting bodies characteristic of the species.

Fig. 3. Map showing the distribution of *P. circinatus*. It will be observed that the species has a predominantly northern distribution.



1 2



3 Map showing the North American distribution of Polystictus circinatus Fr.
● References from literature; ▲ Specimens from Farlow Herbarium;
✚ Places where the author's studies were made.

PLATE I

EXPLANATION OF PLATE II

Shadowgraph taken from seedlings of *Picea rubra* and reproduced at one-half of actual size. Specimens on the extreme left of upper and lower row show branching. Note that the inoculated seedlings (below) have longer internodes above the first year node, that the needles are more numerous and that the root system is more robust and for the most part more abundantly provided with secondary rootlets.

PLATE II

EXPLANATION OF PLATE III

Fig. 1. Cross-section of rootlet of *Picea rubra* inoculated with *P. circinatus*, to show the mantle of pseudoparenchymatous tissue and the *Hartig net* which surrounds all the cortical cells.

Fig. 2. Cross-section of rootlet of *Picea mariana* from rootlet nest from which the sporophore of *P. circinatus* had arisen. Notice the distinct pseudoparenchymatous mantle at the left, and the beginning of the formation of the *Hartig net*.

Fig. 3. Cross-section of a small root of *Picea mariana* which has begun to show root rot. Note the accumulation of dark tannin globules in most of the cells and also the faintly showing mycelium that has penetrated into the interior of the central cells after having passed through the walls.

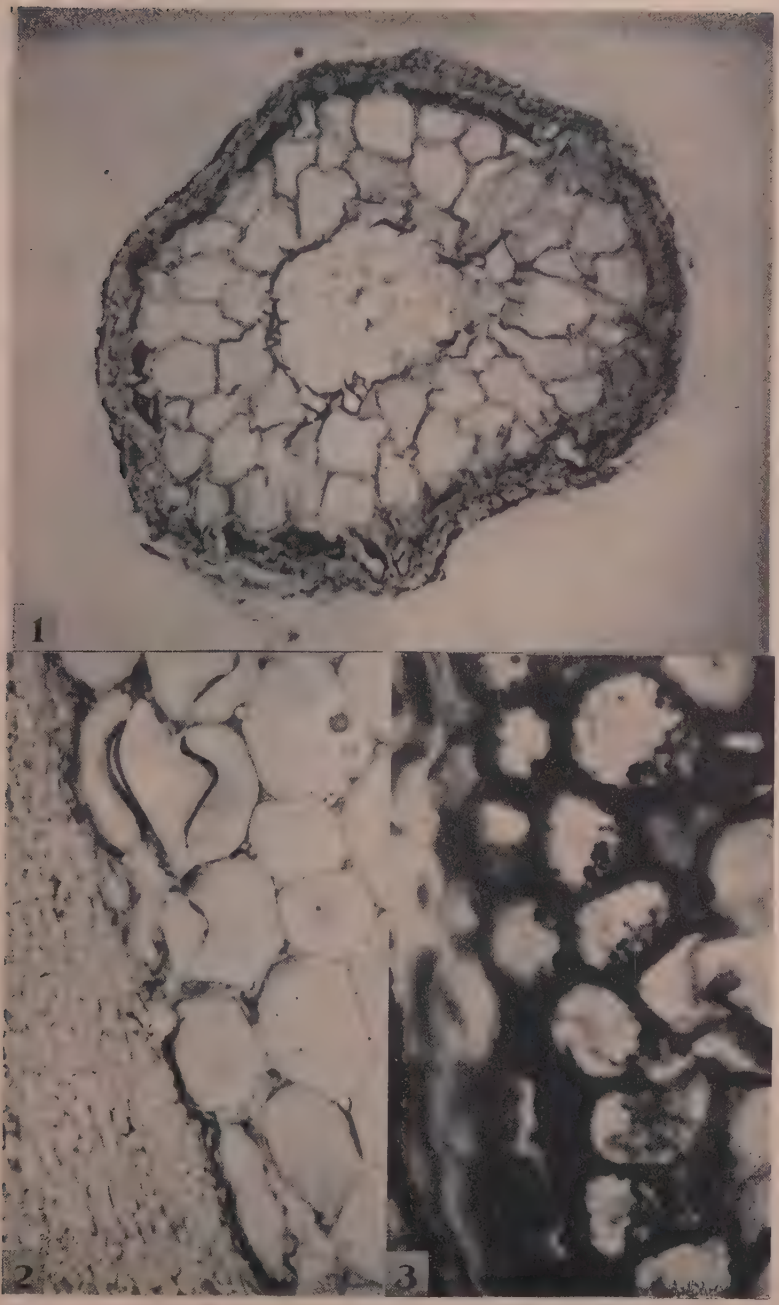


PLATE III

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1(4): 569–581 FARLOWIA July, 1944

NOTES ON WISCONSIN PARASITIC FUNGI. IV.

H. C. Greene

These notes are a continuation of those of the late J. J. Davis who published at intervals on the parasitic fungus flora of the state of Wisconsin for a period covering nearly half a century, from 1893 to 1937. During the latter half of this period Dr. Davis, then retired from medical practice, covered the state so extensively that it seems likely that the plant parasitic fungi of Wisconsin are as well known as those of any other comparable region of the United States. I have, partly from necessity and partly from choice, largely confined my work to intensive collecting in small areas throughout entire seasons. As is known to anyone who has collected in this fashion, the range of parasites that will be encountered over a period of years seems limited only by the host plants which are present. Thus, it has been possible to find many parasitic fungi which are new to the state, and to find an even greater number which, although previously cited, are on host plants not before reported as bearing them in Wisconsin.

The fungi mentioned in the notes which follow were, unless it is otherwise stated, collected in the vicinity of Madison, Dane County, Wisconsin during the season of 1943.

Physoderma Claytoniana sp. nov.

Verrucis purpureo-brunneis, rotundatis, 0.7–1 mm. diam., in foliis, gregariis vel dispersis; sporis levibus, globosis vel subglobosis, aureo-brunneis, 16–23 μ, episporis 1–2 μ crassis.

Galls purplish-brown, rounded, 0.7–1 mm. diam., on leaves, gregarious or scattered; spores smooth, globose or subglobose, yellow-brown, 16–23 μ, epispore 1–2 μ thick.

On leaves of *Claytonia virginica*. Baxter's Hollow, Town of Sumpter, Sauk Co., Wis., U. S. A., April 30, 1938.

There appear to be no previous reports of *Physoderma* on members of the Portulacaceae.

Well-developed perithecia of **Erysiphe graminis** DC. were found on leaves of *Agropyron repens*, July 19. Records of perithecia in Wisconsin are very few and, so far as I am aware, there is none in the case of quack grass. The asci were well formed but contained no spores. The material in the field was examined at intervals over a six weeks period, but spores were not produced.

Dryopteris Thelypteris in marshes about Lake Wingra was heavily infected by **Taphrina lutescens** Rostr. in July. This was determined by Dr. A. J. Mix who (Mycologia **30:** 564, 1938) points out that the asci may be considerably smaller than those of the original Danish form, and this is the case with the Wisconsin collections. Dr. Mix informs me

that only two or three additional collections of **T. lutescens** are known from the Western Hemisphere.

In coöperation with Dr. G. B. Cummins of Purdue University, cultures of **Puccinia Liatridis** (Webber) Bethel from *Koeleria cristata* have been made in the open on various species of *Liatris*, and a reciprocal culture on *Koeleria* obtained.

Arthur (Mycologia **9**: 301, 1917) was the first to publish an account of successful cultures of this rust, on *Liatris punctata*, although Bethel had earlier made similar cultures without publishing his results. Dr. Cummins states that so far as he knows Arthur's is the only cultural work which has heretofore been carried out with **P. Liatridis.**

The current studies have been made in part by Dr. Cummins at Lafayette, Indiana and in part by the writer at Madison, Wisconsin. Aecial material was collected by Dr. Cummins in the field near Ogden Dunes on U. S. Highway 12, east of Gary, Indiana, June 25, 1942. The heavily infected *Liatris spheroidea* was closely associated with *Koeleria cristata* bearing uredia of **P. Liatridis.** On October 22, 1942 Dr. Cummins revisited this location and collected telial material in abundance. (This was overwintered in cheesecloth bags in the open at Lafayette.) At the same time *L. spheroidea* plants were dug and transplanted to plots at Lafayette, along with plants of *L. spicata* and *L. spheroidea* obtained near Monon, Indiana in an area where the rust has not been observed.

Cultures at Lafayette were made by mulching the *Liatris* plants with overwintered telial material on May 5, 1943. Pycnia were observed on all the mulched plants on May 23, followed by aecia on and after June 1, 1943.

The Wisconsin cultures were carried out in similar fashion with telial material furnished by Dr. Cummins. Two species of *Liatris* were employed, *L. squarrosa* and *L. ligulistylis*. The former is not indigenous to Wisconsin, but occurs in an abandoned nursery in the University of Wisconsin Arboretum at Madison. Plants of *L. squarrosa* were mulched on May 19. Pycnia appeared ten days later, but the development of aecia required nearly two weeks more, being slowed by unseasonably cold weather. The culture on *L. ligulistylis* was made on plants which had been transplanted in 1942 some five miles from their native habitat to property owned by the writer near Eagle, in Waukesha County. These were mulched on May 28, 1943. It was not possible to examine them again until three weeks later, at which time well-developed aecia were found on the blades and petioles of the leaves. Only the plants which had been mulched showed the infection, although others of the same species were growing very near them. In this connection it is of interest that naturally infected *L. ligulistylis* was found at the same time in its native locale on the Scuppernong Prairie, two miles northwest of Eagle, Wisconsin.

The reciprocal culture was made by bringing a potted tuft of un-

rusted *Koeleria cristata* into contact with rusted *L. squarrosa* in the field. After approximately a month, both uredia and telia developed on leaves proliferated from the base of the clump. Other clumps of *Koeleria*, growing at the place where the experimental one was obtained, were examined at intervals throughout the summer without showing any signs of rusting.

Specimens of all these cultures have been deposited in the Arthur Herbarium at Purdue University and in the Cryptogamic Herbarium of the University of Wisconsin.

The names of the host species are based in part on a paper by L. H. Shinners entitled "A Revision of the *Liatris scariosa* Complex" (Amer. Mid. Nat. **29:** 27–41, 1943). We are indebted to Dr. Shinners for the determination of the Indiana specimens.

In the Wisconsin Herbarium there are aecial collections of **Puccinia Liatridis** on seven species of *Liatris*, namely, *L. cylindracea*, *L. ligulistylis*, *L. punctata*, *L. pycnostachya*, *L. spheroidea*, *L. spicata* and *L. squarrosa*. So far as I am aware no collections on *L. cylindracea*, *L. ligulistylis*, or *L. pycnostachya* have been made outside Wisconsin up to the present.

Puccinia Helianthi Schw. I on *Helianthus rigidus*. (*H. scaberrimus* of Gray's Manual, 7th ed), June 12. Aecia of **P. Helianthi** are rarely developed in Wisconsin. On *H. rigidus* they are very inconspicuous and small, being confined to a single cup in extreme cases. The only other aecial collections on this host in the Wisconsin Herbarium are No. 2961 of Fungi Columbiani, taken at Scotia, Nebraska, June 1909, and No. 2043 of North American Uredinales from Brownlee, Nebraska, July 1918. Dr. Cummins states that there are likewise no other specimens on this host in the Arthur Herbarium.

Some species of orchids grown in greenhouses are very susceptible to attack by *Gloeosporium*. A leaf die-back is the common result, with the tips being first involved, and the infection then spreading back toward the base, until ultimately the entire leaf may be killed. Rather cursory inspection of plants in greenhouses at and near Madison revealed the following orchids suffering from this disorder: *Bulbophyllum Ericksonii*, *Cattleya autumnalis*, *Cattleya Loddigesii*, *Cochlioda vulcanica*, *Cymbidium longifolium*, *Cymbidium Tracyanum*, two *Cymbidium* hybrids, *Laelia Perreni*, *Laelia tenebrosa*, *Maxillaria tenuifolia*, *Maxillaria variabilis*, *Odontoglossum Schlieperianum*, *Odontoglossum crispum* hybrid, *Odontoglossum eximum* hybrid, *Ornithidium densum*, *Phaius maculatus*, two *Phalaenopsis* hybrids, *Saccolabium ampullaceum*, *Stelis* sp. and *Trichopilia fragrans*. Provisionally these infections are all regarded as being caused by **Gloeosporium cinctum** B. & C. While there is considerable variation in the shape and size of individual conidia, there nevertheless seems to be a definite intergradation. However, in view of the diverse origins of the host plants, it may well be that more than one species of

Gloeosporium is involved. If so, morphological characters do not seem to be well enough defined to offer any certain means of differentiation. (**Gloeosporium** sp. on *Epidendrum atropurpureum* var. *roseum* has spores considerably wider (up to 7 μ) than most of the other forms which I have more or less arbitrarily assigned to **Gl. cinctum.** It may be that this is **Gl. Oncidii** which I have previously reported on *Oncidium sphacelatum.* That report was based primarily on the host, however, and it was noted at the time that **Gl. cinctum** and **Gl. Oncidii** seemed to intergrade. **Gloeosporium** sp. on *Aerides Houlletianum* has conidia which are of the dimensions of those described on **Gl. cinctum,** but on *Aerides* the hyaline conidia are produced on a compact, pulvinate, dematiaceous stroma which forces the smooth unruptured epidermis upward, so that the acervulus appears as a shining black hemisphere on the leaf surface. Various species of *Gloeosporium* have been described on orchids, but the exotic nature of most of the hosts and the similarity of most of the descriptions combine to create uncertainty in the observer seeking to identify species. It seems obvious that until much more material has been collected and studied, identifications of many fungi on greenhouse orchids must be tentative.)

Asteromella astericola J. J. Davis has been found on *Aster ericoides* (*Aster multiflorus* of Gray's Manual, 7th ed.). Davis (Trans. Wis. Acad. Sci. **21:** 281, 1924) described this species on *Aster lateriflorus* from Blue River, Grant County, as follows: "Pycnidia epiphyllous on indefinite purple areas in compact orbicular groups, black, globose, 100–165 μ diam.; wall parenchymatous of dark firm cells 6–10 μ in diameter; sporules sessile (?), hyaline, terete to fusoid-cylindrical, mostly straight, 20–30 x 3–4 μ." This organism seems to me to be of highly dubious status. It is decidedly reminiscent of so-called **Rosenscheldia Heliopsidis** (Schw.) Theiss. & Syd. on various species of *Helianthus* and *Aster.* In my specimen a considerable proportion of the very large spores show a medium septation, and I find that Davis' specimens show this character even more pronouncedly. Why Davis failed to observe this I do not know. At any rate this would seem to remove the organism from *Asteromella* as defined. Davis suggests that this may be a better developed form of **Asteromella Asteris** Peck which, however, has much smaller spores, 6–8 x 2–2.5 μ, and continuous.

In this connection, on leaves and portions of living stems of *Helianthus strumosus* (Madison, Wis., June 1938) I made a large collection of what was taken in the field for **Rosenscheldia Heliopsidis.** The material was examined and, as expected, was sterile. Only one or two mounts were made, from lesions on the stem, which appeared more mature than those on the leaves. The specimen was filed and not re-examined until recently, when one of the leaf lesions was sectioned. Surprisingly it bore the clustered pycnidia of a well-developed *Phyllosticta* with relatively large subglobose spores. It was found that a small

number of the supposed immature *Rosenscheldia* perithecia likewise contained conidia. A specimen on *Helianthus* sp. collected by Davis at Ferry Bluff, Sauk County, shows the same characters in so far as the leaf lesions are concerned. Like myself, Davis apparently did not examine the leaf spots, and he put the specimen in the herbarium as sterile **R. Heliopsidis.** Davis (Trans. Wis. Acad. Sci. **9:** 172, 1893) reported **Phyllosticta Helianthi** Ell. & Ev. on *Helianthus* sp. from Racine County. So far as I have been able to determine no such species has been published. It seems possible that Davis sent a specimen to Ellis who gave the fungus this name, and then neglected to publish it. There is no specimen at the University of Wisconsin. A brief description of the recent material is as follows: Leaf spots brownish, rounded, 0.5–2 mm. diam.; pycnidia epiphyllous, gregarious or crowded in a thin brown stroma, erumpent or deeply immersed, globose or subglobose, 65–165 x 50–120 μ diam., ostiole 15–20 μ diam.; conidia hyaline, subglobose to ovoid, 6–12 x 5–8 μ; conidiophores slender, very short. All these forms are similar externally, but their relation, if any, to one another and to **Rosenscheldia Heliopsidis** is obscure and will require further study.

Phyllosticta guttulatae Hals. on *Oxalis stricta.* June 18. This species has distinctively biguttulate spores and is notable in that on this host the pycnidia are frequently most numerous on the crown and even occur on some of the smaller roots. They also occur on the stems and petioles, but very sparsely on the leaves. In the original description, based on material on "*Oxalis corniculata* var. *stricta*," the leaves only are indicated as the substratum. In a later specimen on *Oxalis europea* (*O. corniculata* of Gray's Manual, 7th ed.) the leaves only are infected. This fungus has not been reported from Wisconsin before.

It appears from examination of specimens of *Phyllachora oxalina* Ell. & Ev. (Jour. Myc. **3:** 41, 1887), described on the basis of a conidial stage only, that it is the same thing as *Phyllosticta guttulatae*, the latter published May 1, 1893 by means of a printed label (Seymour & Earle, Economic Fungi No. 271). Dearness (Mycologia **16:** 155, 1924) reported finding an ascigerous stage on the stromatically blackened stems of plants which had earlier borne the stylosporous stage. He assumed that the two are connected, but offered no proof therefor, and so far as I have been able to determine such connection is still unsubstantiated. It seems to me that Halsted's name should continue to be used for the present.

Phyllosticta solidaginicola sp. nov.

Maculis conspicuis, cinereo-brunneis, cum marginibus fuscis, centris cinereis plusve minusve, orbicularibus, 2–10 mm. diam., plerumque 5 mm.; pycnidiis atro-brunneis, muris tenuibus, subglobosis vel late ellipticis, 100–200 μ diam., subepidermidibus, epiphyllis; conidiis angustis-cylindraceis, rectis vel leviter curvatis, 5–7 x 1.5–2 μ; conidiophoris angustis, confertis, prope obsoletis.

Spots conspicuous, grayish-brown, with narrow dark brown margin, center more or less cinereous, orbicular, 2–10 mm. diam., mostly about

5 mm.; pycnidia blackish-brown, thin-walled, subglobose or broadly elliptical, 100–200 μ diam., subepidermal, epiphyllous; conidia slender-cylindric, straight or sometimes slightly curved, 5–7 x 1.5–2 μ; conidiophores slender, closely ranked, almost obsolete.

On leaves of *Solidago serotina*. Madison, Wis., U. S. A., August 16, 1943.

This was abundant on *Solidago serotina* in marshes in the vicinity of Madison in the 1943 season and a number of collections were made. I have not seen it in previous years in the same area. Had it been present in quantity it could scarcely have escaped notice. Occasional pycnidia are somewhat larger than indicated in the description.

Phyllosticta Solidaginis Bres. on *Solidago serotina* occurred associated with **Ph. solidaginicola,** but the two seem distinct. **Ph. Solidaginis** was rather inadequately described by Bresadola, but the Madison specimen appears to be much the same thing as No. 2377 of Krieger's Fungi saxonici which should be authentic. Descriptive notes on the Wisconsin material are as follows: Spots large, faintly zonate, rounded on the inner side, extending to leaf margin on the other, grayish brown; pycnidia dark brown, numerous flattened, subepidermal, epiphyllous, narrowly ostiolate, 50–130 μ diam., mostly 75–100 μ; conidia hyaline, ellipsoid, 2.5–3.5 x 4–6 μ. Bresadola reports narrower conidia for this species but I find those of the Krieger specimen to be about of the dimensions given above.

Neottiospora arenaria Syd. on *Carex rostrata.* September 25. Sydow described this unusual species from overwintered material, collected in May, and thus it was not possible to judge whether or not the fungus had developed parasitically. The present specimen was collected from living plants with many healthy green leaves. Some of the leaves bearing the fungus were still partially green, although most had died down completely. It appears possible that the organism is at least weakly parasitic, and if it was the primary agent it is a destructive parasite. The spherical carbonaceous pycnidia are borne almost free in the chambers of the disintegrating host tissue. Under a hand lens the pycnidia look like sclerotia, each resting on a small weft of dark mycelium.

Sphaeropsis foliicola (Berl. & Roum.) Sacc. on *Crataegus* sp. September 11. Coll. M. P. Backus. Berlese and Roumeguere in their description of **Sphaeropsis demersa** (Bon.) Sacc. var. **foliicola** Berl. & Roum. (Rev. Mycol. **9:** 163. 1887) state that the pycnidia are on pale yellow spots. Here they are on well-defined silvery gray, orbicular spots, about 2–3 mm. diam. The silvery tinge seems to be due to the cuticle, for a later specimen where this has fallen away has spots with a sordid yellowish color. In microscopic characters this corresponds well with Fungi Columbiani No. 4687, issued as **S. foliicola.**

In June 1938, near Lodi, Columbia County, leaves of *Panicum virgatum* were found bearing what appeared to be the elongated uredia of a rust, light tan in color. However, microscopic examination disclosed what seemed to be a species of *Sporonema* with long-chambered, ramifying pycnidia. A description was prepared, but not published because of the small size of the original collection, and the seeming entire lack of reports of *Sporonema* on Gramineae. The descriptive notes are as follows: Pycnidia epiphyllous, pale brown, elongate, scattered or closely ranked, imperfectly formed, splitting open above, tending to be internally divided, 200–500 μ long x 75–125 μ diam., somewhat flattened; conidiophores hyaline, simple and unbranched, slender, 5–6 μ long, or sometimes almost obsolete, closely crowded over all inner surfaces of the fruiting body; conidia hyaline, ellipsoid to subcylindrical, 4–8 x 3–3.5 μ, mostly 6–7 x 3 μ. In September 1942 and in August 1943 collections of supposed **Phyllachora graminis** were made on *Panicum virgatum* at Madison. No *Phyllachora* asci were found, and Professor Orton informs me that this is the usual case with material on *Panicum virgatum*. It was noted that most of the black stromata had whitish "blisters" on top, and that these were pierced by a rather definite, more or less elonganted pore. Sections show a basal sporiferous layer with small conidia, identical with those of the supposed *Sporonema*. It seems probable therefore that the "*Sporonema*" is but an early stage in the development of the tar spots. (Professor Orton states that he has several specimens of *Phyllachora* on *P. virgatum* with mature asci and spores, and that, although conidial stages were found with some of these, phylogenetic relationships remain to be proved.)

On various grasses in the vicinity of Madison, there have been found specimens of what may be a single species of a coarse-spored *Stagonospora*. The pycnidia are rather large, erumpent, with spores about of the order of 30–35 x 10–12 μ, several septate and markedly guttulate. These have been observed on *Sorghastrum nutans*, *Andropogon furcatus*, *Panicum Scribnerianum* and *Phragmites communis*. Dr. Sprague tells me that he has found a similar fungus on *Calamovilfa longifolia* at Mandan, North Dakota. **Stagonospora Paspali** Atk., described on *Paspalum laeve* from Alabama, and **S. simplicior** Sacc. & Berl. f. **Andropogonis** Sacc., described as on dead stems of *Andropogon furcatus* from North Dakota, seem very close to the Wisconsin collections. On *P. Scribnerianum* and on *A. furcatus* there are well-defined spots. On *S. nutans* the pycnidia occur seriately on rather elongate, poorly delimited lesions, while on *P. communis* most of the leaf is involved. Whether, as suggested, a single species of *Stagonospora* is concerned is probably determinable only by cross inoculations, so far not possible.

Septoria Thlaspii sp. nov.

In fructificationibus, maculis nullis, pycnidiis subepidermidibus, pallidis brunneis, numerosis, gregariis, subglobosis, rostratis, late ostiolatis, 65–100 μ diam.; conidiis

hyalinis, angustis, rectis vel leviter curvatis, sursum angustioribus, 2–3-septatis, 20–35 x 2 μ.

On silicles, no definite spots; pycnidia subepidermal, pale brown, numerous, gregarious, subglobose, rostrate, widely ostiolate, 65–100 μ diam.; conidia hyaline, slender, straight or slightly curved, tapered distally, 2–3-septate, 20–35 x 2 μ.

On partially ripened silicles of *Thlaspi arvense.* Dane Co., near Sauk City, Wis., U. S. A., July 10, 1943.

Associated with this is a microconidial form, perhaps the precursor of a perfect stage. There seems to be no previous report of *Septoria* on any species of *Thlaspi,* in America or in Europe.

Septoria Andropogonis var. **Sorghastri** Greene & Sprague var. nov.

Sporulis filiformibus, 3–9 septatis, hyalinis, 50–100 x 1.5–2.5 μ.

In foliis vivis *Sorghastri nutantis.* Madison, Wis. (typus) et Long Pine, Nebr., U. S. A.

Septoria Andropogonis was described by Davis from Wisconsin material (Trans. Wis. Acad. Sci. **18** (1): 88, 1915) as having the sporules 2–4 septate, 30–50 x 2–3 μ. Thus, the fungus on *Sorghastrum* differs from the species proper in having much longer, multiseptate, curved sporules. While at first glance the spores of the variety appear distinct from those on *Andropogon* the difference appears to be largely due to the addition of septa and increase in length of the spores with accompanying crowding in the pycnidia. This condition may be partly brought about by tardily formed ostioles in var. **Sorghastri.**

Rev. J. M. Bates collected this fungus at Long Pine, Nebraska, Sept. 13, 1899, while one collection which we are making the type has been made recently at Madison, Wis.

Septoria emaculata Peck & Clint. on *Lathyrus palustris* var. *linearifolius.* Waukesha County, Eagle, August 8. This interesting species, new to Wisconsin, was taken accidentally in the course of collecting specimens of **Uromyces Fabae.** As the name indicates, there is no spotting whatever, and the pycnidia are remotely and evenly dispersed in a fashion that is reminiscent of the pycnia of **Tranzschelia Pruni-spinosae.**

A fungus which is morphologically identical with **Phaeoseptoria Calamagrostidis** Sprague, described in a recent article (Mycologia **35:** 487, 1943) has been found at Madison on *Calamagrostis canadensis.* A specimen was submitted to Dr. Sprague who confirms the determination. The Madison material, however, has the *Phaeoseptoria* borne in, or in close connection with, *Phyllachora*-like lesions, which was not the case with the Oregon fungus on which the description was based. These lesions are much like those produced in char-spot of certain western grasses, caused by **Septogloeum oxysporum** Sacc., Bomm. & Rouss. and discussed extensively by Sprague in an article entitled "A Blotch and Char-Spot of Western Grasses," (Northwest Science, Nov. 1941). Im-

perfect pycnidia which contain spores somewhat similar to those of **S. oxysporum** have been found in lighter areas adjoining the char-spots. Dr. Sprague states, however, that he would hesitate to assign these to **S. oxysporum** since the spores do not seem quite typical.

A curious and well-marked species is **Dilophospora Alopecuri** Fr. found on *Calamagrostis canadensis*. Davis reported this for Wisconsin on the basis of an illustrated article by E. A. Bessey (Jour. Mycol. **12**: 57, 1906). Davis had sent leaves of the grass to Bessey, who wished to study nematode action, and Bessey discovered the fungus, apparently in small quantity, for there is no specimen at Madison. In the recent specimen the pycnidia are on narrow, elongated, arid lesions.

Cylindrosporium triflori sp. nov.

Maculis pallidis brunneis, cum centris aliquanto fuscioribus, depressis, marginibus angustis, fuscis; maculis cum halis rubellis-purpureis, paucis vel multis, raro confluentibus, rotundatis, 1.5–3 mm. diam., plerumque ca. 2 mm.; acervulis numerosis, gregariis, epiphyllis, parvulis, 40–60 μ, plerumque ca. 50 μ diam.; conidiophoris brevissimis, confertis in stromatis flavido-brunneos; conidiis filiformibus, hyalinis, saepe septatis indistincte, 35–65 x 1.5–2.5 μ.

Spots pale brown with centers somewhat darker, sunken, border narrow, dark brown; spots surrounded by discolored reddish-purple host tissue, few to many, rarely confluent, rounded, 1.5–3 mm. diam., mostly about 2 mm.; acervuli numerous, gregarious, epiphyllous, small, 40–60 μ, mostly about 50 μ diam.; conidiophores very short, aggregated into erumpent yellowish-brown stromata; conidia filiform, hyaline, often indistinctly septate, 35–65 x 1.5–2.5 μ.

On leaves of *Geum triflorum*. Scuppernong Prairie, two miles northwest of Eagle, Waukesha Co., Wis., U. S. A. Coll. H. C. Greene & M. P. Backus. August 8, 1943.

This seems distinct from **Cylindrosporium Gei** Farl. which is amphigenous and is a decidedly coarser form. The spots show distinctly on both sides of the leaf, but the acervuli are borne only on the upper surface. This has also been collected near Mazomanie in Dane County, Wisconsin.

A large species of *Botrytis* of the **B. cinerea** type has been observed in an interesting relationship to **Puccinia rubigo-vera** (DC.) Wint. I on *Thalictrum dasycarpum*. The *Botrytis* overgrew the hypophyllous aecia and apparently was responsible for the necrosis of adjacent tissues of the leaf. The necrotic areas extend well beyond the limits of the aecia and are plainly not due to the action of the rust. Probably the *Botrytis* gained a foothold on the tissues killed by the rust and then functioned as a weak parasite.

Elongated lesions bearing *Fusarium* were observed on stems of wilted plants of *Astragalus canadensis*, July 28. Fresh material was sent to Dr. William C. Snyder of the Division of Plant Pathology at the Uni-

versity of California. Dr. Snyder kindly made single spore cultures and found **Fusarium moniliforme** and **F. tricinctum,** or a closely related species, to be present. He stated that as **F. moniliforme** was present in abundance, and since it is somewhat parasitic on several hosts it may be considered as a possible primary agent. He suggests that another possibility that deserves consideration is that the wilting may have been caused by one of the necrotic or streak viruses, and that the fungi occur as secondary parasites. This has occurred on certain leguminous plants in California.

A find of considerable interest is **Dicoccum nebulosum** Ell. & Ev. on *Fraxinus americana* in a nursery in the University of Wisconsin Arboretum. Ellis and Everhart based their species on material from Somers, Kenosha County, Wisconsin, collected by Davis in 1893. A specimen which is presumably part of the type is in the Davis Herbarium, but no other collections from Wisconsin or elsewhere are in the University Herbarium.

Cercoseptoria Blephiliae sp. nov.

Maculis angulatis, indefinitis, frequenter 5 mm. latis, melleis, immarginatis, limitatis pars interioribus venis amplioribus; conidiis hypophyllis, hyalinis, confertis, numerosis, acutisculis, frequenter obscure 6–8 septatis, plerumque curvatis, granulosis, 35–80 x 3–4 μ; tuberculis infra stomatibus, gibbis, 20–40 μ diam., cum olivaceis, pseudoparenchymatibus cellis, 6–8 μ diam.

Spots angular, indefinite in extent, often about 5 mm. wide, pale yellow, immarginate, limited by the larger veins; conidia hypophyllous, hyaline, massed, numerous, tapered, often obscurely 6–8-septate, usually curved, granular, 35–80 x 3–4 μ; tubercles substomatal in origin, convex, 20–40 μ diam., composed of olivaceous, pseudoparenchymatous cells 6–8 μ diam.

On leaves of *Blephilia ciliata.* Madison, Dane Co., Wis., U. S. A., June 25, 1943.

The lower leaf surface where the conidia are massed is a dead white and the presence of individual fascicles is not apparent from a hand lens inspection. The tubercles become intrastomatal, as it were, for they protrude up through the stomata. **C. Blephiliae** has also been found on *Pycnanthemum virginianum* in the same vicinity where the original collection was made on *Blephilia.* The general appearance is the same, although fewer conidial tufts per unit area are produced on *Pycnanthemum.* The microscopic aspect is identical. So far as one can judge from the inadequate description, it seems possible that this is close to Atkinson's **Cercosporella Pycnanthemi,** described as on *Pycnanthemum* sp. in Alabama.

A most distinctive fungus has been found on living stems of *Equisetum laevigatum.* After considerable study I have decided that it is best placed under **Ramularia Equiseti** C. Mass., although it diverges in some respects from that species as described. The spots produced on the stems

are extremely irregular, wavy, resembling the most imaginative camouflage. The stem of *E. laevigatum* is highly silicified, with straight longitudinal rows of sunken stomates. These stomates are developed between the ridges of the stem and over the patches of green mesophyll which are interspersed at regular intervals between masses of mechanical tissue. The fungus produces a yellow-brown, globose stroma beneath each of the stomates within an infected area. From each stroma there is produced upward through the stomate a fascicle of rather long subclavate conidiophores which spread out fanwise at the surface of the stem. The conidiophores show a single apical scar. They are hyaline, subclavate, 50–60 x 5–6 μ, non-septate or 1-septate. The hyaline conidia are of two types (1) 40–65 x 7 μ, 2–3-septate, distinctly clavate, tapering to a width of 4 at the apex, and (2) 25–35 x 7 μ, non-septate to 2-septate, cylindrical. It seems possible that the shorter cylindrical conidia are but incompletely developed. July 8, 1942. Also collected in 1943.

Professor Chupp states that the *Cercospora* on *Barbarea vulgaris* which was named by Saccardo **C. Nasturtii** var. **Barbareae** does not resemble any of the other species reported on the Cruciferae. Therefore, with Professor Chupp's authorization the species is here listed as **Cercospora Barbareae** (Sacc.) Chupp n. comb.

A new species of *Cercospora* which occurred on *Bouteloua curtipendula* is described as **Cercospora Boutelouae** Chupp & Greene.

Cercospora Boutelouae sp. nov.

Maculis anguste ellipticis vel elongatis, 0.5–4 mm. longis, brunneis pallidis vel tantum non nigris, immarginatis vel cum halis ochraceis; fructificationibus maxime hypophyllis, in seriebus; stromatibus nullis vel cum paucis cellis brunneis; fasciis 2–14 cauliculis divergentibus; conidiophoris pallidis mediisve brunneis, leviter pallidioribus et angustioribus ad apices, paucis septatis, non ramosis, 0–1 praerupte geniculatis, rectis vel curvatis, apicibus subtruncatis, 3.5–5 x 20–100 μ; conidiis hyalinis, obclavatis, leviter curvatis, indistincte multiseptatis, basibus longis obconicis truncatis, apicibus subobtusatis, 3.5–5 x 20–80 μ.

Spots narrowly elliptic to elongate, 0.5–4 mm. in length, pale brown to almost black, immarginate or with a yellowish halo; fruiting mostly hypophyllous, seriate; stromata lacking or only a few brown cells; fascicles 2–14 spreading stalks; conidiophores pale to medium brown, slightly paler and narrower near the tip, sparingly septate, not branched, 0–1 abruptly geniculate, straight to curved, tip subtruncate, 3–5.5 x 20–100 μ; conidia hyaline, obclavate, mildly curved, indistinctly multiseptate, base long obconically truncate, tip subobtuse, 3.5–5 x 20–80 μ.

On leaves of *Bouteloua curtipendula*, Madison, Wis., U. S. A., July 26, 1943. Coll. H. C. Greene.

A new species of *Cercospora* which occurred on *Alnus crispa* is described as **Cercospora Alni** Chupp & Greene.

Cercospora Alni sp. nov.

Maculis indistinctis. fructificationibus hypophyllis, effusis, fusco-olivaceis, parvis, irregularibus, 0.5–5 mm. longis; stromatibus nullis vel tantum paucis fuscis cellis, fasciis compactis vel diffusis, 3–20 cauliculis; conidiophoris cumulis fuscis, singillatim pallidis vel modicis olivaceo-brunneis, apicibus nonnihil pallidioribus, irregularibus vel clavatis, obscure multiseptatis, raro ramosis, sursum confertim undulatis vel multigeniculatis, apicibus obtusis, rotundatis, 3–5.5 x 25–90 μ; conidiis pallidis vel pallidissimis olivaceis, obclavato-cylindraceis, plerumque 1-septatis, cellis inferioribus saepe inflatis, rectis vel minimis curvatis, basibus longis obconicis truncatis, apicibus obtusis, 3.5–5 x 20–60 μ.

Leaf spots none or indistinct; fruiting hypophyllous, effuse, dark olivaceous, in small irregular patches, 0.5–5 mm. long; stromata lacking, or composed of only a few dark brown cells; fascicles compact to spreading, 3–20 stalks; conidiophores in mass dark in color, singly pale to medium olivaceous-brown, somewhat paler near the tip, irregular in width or clavate, indistinctly multiseptate, rarely branched, top half closely undulate or multigeniculate, tip rounded bluntly, 3–5.5 x 25–90 μ; conidia pale to very pale olivaceous, obclavate-cylindric, mostly 1-septate, often with bulging lower cell, straight to slightly curved, base long obconically truncate, tip obtuse, 3.5–5 x 20–60 μ.

On leaves of *Alnus crispa*. Winneboujou, Douglas Co., Wis., U. S. A., September 3, 1942. Coll. J. W. Thomson.

The list which follows is of parasites on hosts which, so far as known to me, have not been previously reported (from Wisconsin or elsewhere) as bearing the fungi concerned:

Synchytrium aureum Schroet. on *Viola sagittata*. Sauk Co., Town of Sumpter, Baxter's Hollow, April 30, 1938.

Peronospora alta Fckl. on *Plantago Purshii*. Dane Co., Madison, June 21.

Puccinia Eleocharidis Arth. III on *Eleocharis acicularis*. Dane Co., Madison, September 25.

Puccinia Andropogonis Schw. I on *Polygala polygama*. Douglas Co., T44N, R12W, S1, SW¼, July 23, 1929. Coll. L. R. Wilson. This is **P. Andropogonis** var. **Polygalina** of Arthur's Manual, hitherto known only on *Polygala senega*. The rust was found in small quantity on the stem of a phanerogamic specimen of *P. polygama* in the University of Wisconsin Herbarium.

Ascochyta Thaspii Ell. & Ev. on *Zizia cordata*. Waukesha Co., Scuppernong Prairie, 2 miles northwest of Eagle, August 8.

Septoria Anemones Desm. on *Anemone cylindrica*. Dane Co., Madison, June 17; also from Waukesha Co., Eagleville, June 20. Ellis and Everhart described **Septoria cylindrica** on this host with fusoid-cylindrical spores, 25–35 x 2½–3 μ. These collections, however, have spores 16–20 x 1 μ, slightly shorter than those of **S. Anemones** as described.

Davis (Trans. Wis. Acad. Sci. **18** (1): 103, 1915) described provisionally the new species **Septoria Senecionis-aurei** on *Senecio aureus*, stating that its relationship to other species, such as **S. Senecionis-sylvatici** Syd., was uncertain. A similar form has recently been found on *Senecio balsamitae* and is assigned to **S. Senecionis-aurei.** It does not correspond well with other species described on *Senecio*. Dane Co., Madison, September 9.

Septoria Cacaliae Ell. & Kell. on *Cacalia suaveolens*. Dane Co., Black Earth, August 3. Davis (Trans. Wis. Acad. Sci. **21**: 288, 1924). states that the *Septoria* which occurs on *Cacalia atriplicifolia* in Wisconsin has spots with a more or less broad dark purple border like those of **S. Nabali** B. & C., but that the single specimen on *Cacalia reniformis* has brown spots with a narrow darker border. The collection on *C. suaveolens* is similar to that on *C. reniformis*. The spores are very short, mostly scarcely more than 20 μ, while those on *C. reniformis* approach 30 μ.

Cercospora Violae Sacc. on *Viola pedata*. Dane Co., Madison, September 9. Many of the leaves of this early flowering species which are produced in the course of the summer undergo great development, becoming much expanded and succulent, presenting a favorable substratum for the development of parasites.

Cercospora gentianicola Ell. & Ev. on *Gentiana procera*. Dane Co., Madison, September 29. This collection shows very close correspondence with the species description (Jour. Myc. **4**: 2, 1888) based on material on the nearly related *Gentiana crinita*.

Cercospora incarnata Ell. & Ev. on *Asclepias verticillata*. Dane Co., Madison, July 26. Determined by Professor Chupp. The infected leaves become a bright yellow in strong contrast to the normal green foliage. **C. incarnata** is new to Wisconsin.

Cercospora briareus Ell. & Ev. on *Acerates lanuginosa*. Dane Co., Madison, June 25. Determined by Professor Chupp.

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A DISCUSSION OF TAXONOMIC CRITERIA IN THE CHYTRIDIALES

Alma J. Whiffen [1]

In his recent book, "Aquatic Phycomycetes," Sparrow, in accord with his own earlier studies (Sparrow, 1935) and those of Scherffel (1925), Couch (1941), and Karling (1942), has eliminated from the Chytridiales all forms not possessing a uniflagellated zoospore. More recently Karling (1943) has proposed the removal from the order of all species with anteriorly uniflagellated zoospores. Therefore, as now characterized, the order Chytridiales consists of a rather homogeneous group of fungi having in common a posteriorly uniflagellated zoospore. Sparrow's taxonomic treatment of the chytrids will be used as the starting point for the discussion in this paper, since his classification, incorporating as it does his own contributions and those of other students of the chytrids, represents so very adequately a summary of our present knowledge of the chytrids.

Students of the chytrids have been so impressed with the incompleteness of our present knowledge of this group of fungi that they have shown great hesitation, but often rightly so, in making any generalized statements concerning the group as a whole. In this way, preferring to reserve discussion of the inter-relationships of the chytrids until more is known about these organisms, we have not utilized the full possibilities of our present knowledge of the chytrids in establishing the foundations of a natural system of classification, which though incomplete and subject to much revision, will show us what must yet be learned about these fungi. From what we now know of the chytrids, it is clear that any system of classifying them will be one of the many possible combinations of the following key characters depending on 1) whether the zoosporangium arises from the enlargement of the zoospore body or from the enlargement of the germ tube from the body of the zoospore; 2) whether a single thallus consists of one or more than one reproductive body; 3) whether or not there are specialized vegetative structures (rhizoids) attached to the reproductive body; 4) whether the zoosporangium is operculate or inoperculate; 5) whether the resting body is sexually or asexually formed; and 6) whether the resting body in germinating functions as a zoosporangium or as a prosporangium. It is now necessary to choose from the above list the characters to be used in classifying the chytrids and to decide upon the relative emphasis to be put upon each character that is selected.

Sparrow makes a primary division of the Chytridiales by recognizing two parallel series: the Inoperculatae, characterized by the absence of an operculum, and the Operculatae, in which an operculum is present. Such a division of the Chytridiales has been effected for the first time by Spar-

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row and may be objected to for a number of reasons. First, the two series widely separate genera which are similar except for the presence of the operculum in the one and its absence in the other. It has been shown (Whiffen, 1943) that when the operculate-inoperculate character is used to separate *Cladochytrium* and *Nowakowskiella*, the result is that in *Cladochytrium* there are placed species which differ from the other members of *Cladochytrium* in just those characters which are identical with those possessed by the species of *Nowakowskiella*. This is but one example of the problem which is presented in a magnified form when the *Chytridiales* are divided into operculate and inoperculate series. Parallel evolution is cited as an explanation of this situation by Sparrow (1943), who states that "the members of the Operculatae and Inoperculatae parallel each other in their methods of development and in their thallus structure." It is just as probable, though, that the operculate character itself is the result of a "parallel development" which appears frequently within closely related groups having similar methods of development and thallus structure.

Furthermore, the members of each series show very little evidence of constituting a group of similar forms as they should if this division of the Chytridiales were a "natural" one. In such a case the validity of the primary character of operculation and inoperculation would be substantiated by the demonstration of secondary characters which contrast with each other and which correlate with the operculate and inoperculate condition, and such characters are not to be found. The heterogeneous nature of Sparrow's operculate Chytridiaceae is well demonstrated by its four sub-families, each containing but one or two genera. In fact, what this division of the order does accomplish is the undesirable segregation of a few genera of the eucarpic monocentric and polycentric chytrids from the eucarpic genera with which they should be associated by virtue of similar thallus form and thallus development. Since none of the holocarpic chytrids is operculate, this division is really applicable to only the eucarpic chytrids in which the operculate condition may be regarded as a localized specialization which is not of importance throughout the whole order.

It may be argued that the use of the operculate-inoperculate character is justified by its constancy and convenience. It cannot be denied that this character is constant but there are other characters just as constant and it may be possible to show that these characters are of greater taxonomic importance than operculation or the lack of it. The convenience of the arrangement may be questioned because of the inherent necessity of increasing the number of families to accommodate the operculate and inoperculate forms.

If we reject the Inoperculatae and Operculatae, it becomes necessary to decide upon some other key character for use in effecting the primary division of the Chytridiales and it is suggested that the holocarpic and

eucarpic character should be so used for the present until a better character can be found. The order would then be divided into a holocarpic group, in which the thallus consists of only the reproductive body, and a eucarpic group, the thallus here consisting of the reproductive body or bodies plus certain vegetative structures such as rhizoids. The three families, Olpidiaceae, Achlyogetonaceae, and Synchytriaceae, included by Sparrow in the holocarpic group, show great diversity in mode of development but have in common their endobiotic parasitic habit which undoubtedly has been responsible in each case for the lack of specialized vegetative structures. It is evident that the holocarpic group is a heterogeneous collection of the products of parasitic specialization and for this reason the affinities of the holocarpic chytrids with the eucarpic chytrids are difficult to ascertain. The clues lie only in a study of the types of thallus development of the holocarpic chytrids. It may then become apparent that certain holocarpic chytrids are more closely related to certain eucarpic chytrids than to other members of the holocarpic group.

We follow Sparrow and Karling in subdividing the eucarpic chytrids into a monocentric and a polycentric group, making this division only once since we would combine the operculate with the inoperculate genera in families defined on the basis of thallus development. In the monocentric group are placed all eucarpic chytrids in which the thallus consists of only one reproductive body while those eucarpic chytrids in which the thallus consists of more than one reproductive body are placed in the group of polycentric chytrids. To state that a polycentric chytrid is one in which a single thallus consists of more than one reproductive body is, however, an over-simplification of the definition of a polycentric chytrid as given by Karling (1932). It would seem that by the term polycentric, Karling designates a condition in which there are several centers of growth where reproductive bodies develop, separated "in space" on what he calls a rhizomycelium. Therefore, strictly speaking, a chytrid with a single primary zoosporangium in which secondary and tertiary sporangia are proliferated would not be called polycentric and would have to be assigned to the monocentric group of chytrids.

In assigning the eucarpic monocentric chytrids to families, Sparrow (1943) makes primary use of the relation of the thallus to the substratum on which it is growing and only secondary use of the type of thallus development. Because of the nature of the parasitic habit, the thallus of a parasitic chytrid does exhibit a high degree of constancy in its positional relationship to its host. It is, therefore, relatively easy to decide whether or not a certain parasitic chytrid is endobiotic with the reproductive body on the inside of the host, exobiotic with the reproductive body on the outside of the host, or interbiotic with the thallus developing attached to several host individuals. So there is little difficulty in assigning the parasitic chytrid to the correct family in Sparrow's classification. A saprophytic chytrid, however, shows great variability in the relation of

the thallus to its substratum and it may be chance alone which will determine whether the zoosporangium of a saprophytic chytrid is to be found on the inside or the outside of its substratum. The identification of a chytrid which is growing in pure culture on agar would not be easy with Sparrow's key.

Sparrow attempts a more effective separation of the epi-endobiotic Phlyctidiaceae from the interbiotic Rhizidiaceae by giving to the Rhizidiaceae the additional characterization in which the reproductive body develops by enlargement of the body of the encysted zoospore. The insertion of this supporting key character for the Rhizidiaceae accomplishes little because there are included in the Phlyctidiaceae species in which the reproductive body also develops directly by the enlargement of the encysted zoospore. Therefore, in determining in which of these two families to place a form in which the zoospore body enlarges into the sporangium, one is immediately thrown back upon the necessity of deciding whether or not the species is endo-, epi-, or interbiotic.

Sparrow subdivides the family Phlyctidiaceae according to whether the zoospore cyst is functional or evanescent and he points out that the genera within each sub-family have similar methods of thallus development and therefore are probably closely related. If this is true, we have here a useful taxonomic criterion. The possibility of classifying the chytrids on the basis of the type of thallus development has already been considered, especially by Karling (1932) and Sparrow (1943), and indeed Sparrow does make use of the developmental types in his key to the chytrid families and sub-families. It is proposed here, however, that eventually the morphogenetic variations among the chytrids should form the basis by which all chytrids are to be classified. Protest is immediate that such a scheme of classification is impossible because in order to identify a chytrid, it would be necessary first to culture it and to observe the germination of the spore and the early stages of the development of the thallus. We admit that for obvious reasons a bacterium must be cultured before it can be identified with certainty and while the case of the chytrid is not as extreme, it is nevertheless similar in that there are so few clear-cut morphological differences among mature thalli of various genera. In actual taxonomic practice, however, the problem is not as difficult as at first it may appear to be. For example, one may become familiar enough with the appearance of the zoosporangia and rhizoids to be able to differentiate between the morphologically similar thalli of species of *Rhizophlyctis* and *Entophlyctis*, two genera in which the type of thallus development is radically different. In order to make workable a classification concerned with thallus developmental types, students of the chytrids must endeavor to fill in the details that are not known about the development of the thallus of the species already described and to determine accurately the developmental type of every new species before describing it. If the premise is correct that genera possessing the same

developmental type are related, it will be possible in time to develop a natural classification of the chytrids by placing together genera with the same type of thallus development. We will now attempt such a classification of the eucarpic monocentric chytrids but to do this we must first discover what types of thallus development are represented by these chytrids.

Sparrow (1943) recognizes in the Chytridiales four types of development, each named for the genus which exemplifies it: 1) *Olpidium*, 2) *Entophlyctis*, 3) *Chytridium*, and 4) *Rhizidium*. The criteria by which these four types are demarcated are but partially morphogenetic and are in the most part concerned with the relation of the thallus to the substratum. The *Olpidium* type is essentially that of the holocarpic chytrids. The *Entophlyctis* type is characterized as endobiotic, the *Chytridium* type as exobiotic, and the *Rhizidium* type as interbiotic. If we take into consideration the endo-exogenous method of development (Karling, 1936), found in *Chytridium* species having prosporangia and regarded by Sparrow as a modification of his *Chytridium* type, then these three types are morphogenetically different. The definition of the thallus developmental types, however, is much clearer if we strip from it all references to the relation of the thallus to its substratum and consider only the morphogenetic aspects. Then five developmental types can be recognized among the eucarpic monocentric chytrids as follows: (see text figure 1)

Group I

Type 1. The encysted zoospore enlarges into a zoosporangium as in *Rhizophydium* or *Rhizidium*.

Type 2. The encysted zoospore enlarges into a prosporangium from which the zoosporangium develops as in *Polyphagus*.

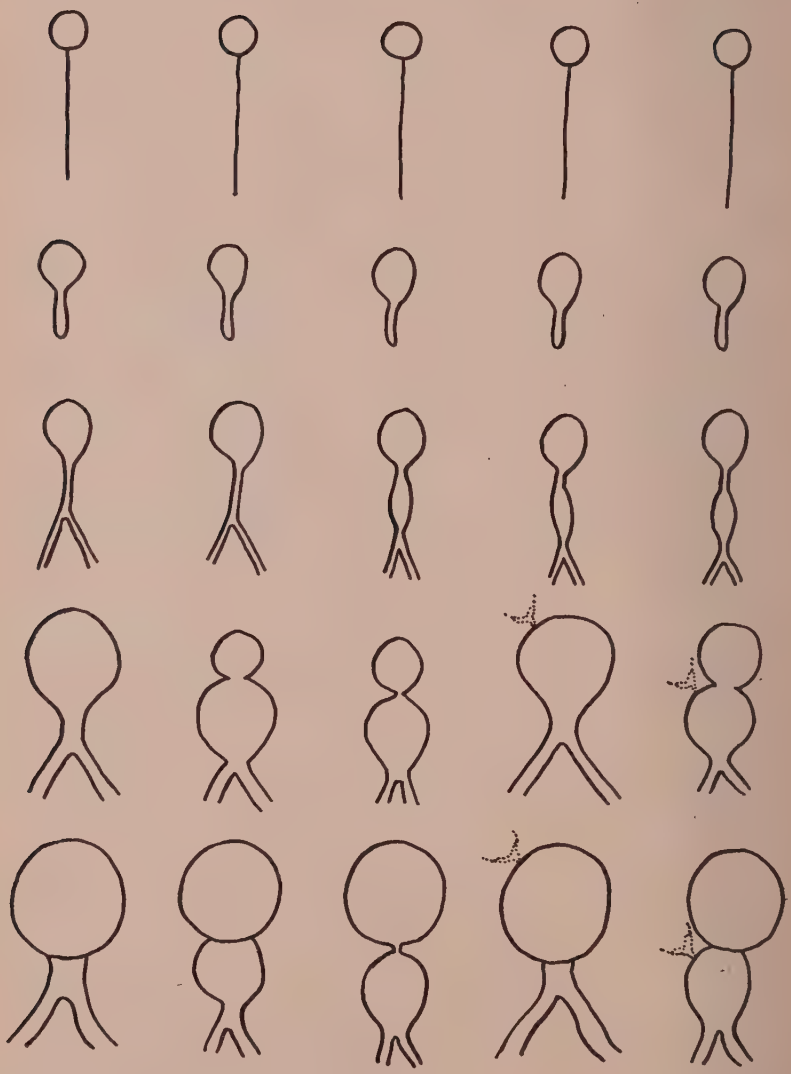
Type 3. A swelling of the germ tube gives rise to a prosporangium that contributes to the subsequent enlargement of the encysted zoospore into a zoosporangium as in *Chytridium Lagenaria*. (The endo-exogenous type of development described by Karling, 1936.)

Group II

Type 4. The zoosporangium develops from an enlargement of the germ tube as in *Entophlyctis*.

Type 5. The zoosporangium develops from a prosporangium which originates as an enlargement of the germ tube as in *Diplophlyctis*.

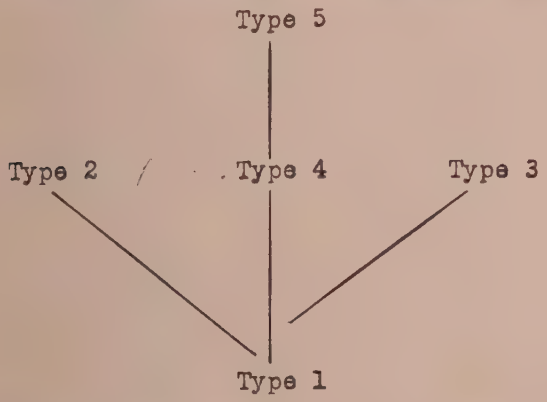
The first three types constitute a group in which the encysted zoospore is functional. In the second group, containing the fourth and fifth types, the encysted zoospore is not functional and the prosporangium or zoosporangium develop instead from the germ tube of the zoospore. As more forms of chytrids are discovered, it will become evident that no sharp line can be drawn between these two groups but on an arbitrary basis it will always be possible to assign a chytrid to one or the other group. If the zoospore body or any portion of it, or the zoospore plus the germ tube takes part in the development of the zoosporangium, the chytrid belongs



TEXT FIGURE 1

in Group I. If the zoospore body becomes completely emptied and no portion of it undergoes further development, then the chytrid is to be placed in Group II. It should be perfectly clear that either the zoospore body or a portion of it does or does not function in the development of the thallus.

Both groups attain the condition in which the development of the zoosporangium is preceded by the establishment of a prosporangium, which arises either from the zoospore itself as in the first group or from the germ tube as in the second group. The prosporangium has frequently been referred to as an apophysis, a term which has been used indiscriminately to describe any subsporangial swelling regardless of whether the swelling originated as a prosporangium or by enlargement of the rhizoidal



TEXT FIGURE 2. The possible derivations of the five developmental types in the eucarpic monocentric chytrids.

axis after the zoosporangium had begun to form. Therefore, in this paper the use of the word apophysis is avoided by the substitution of the terms prosporangium and subsporangial swelling in their proper places. It will be noted that, even though the prosporangium develops from the germ tube, the endo-exogenous type of development is included in the first group because the encysted zoospore still remains functional.

TEXT FIGURE 1. Diagrams of successive developmental stages, illustrating the five types of thallus development in the eucarpic monocentric chytrids.

Family				
Rhizidiaceae			Entophlyctaceae	
Subfamilies				
Rhizidioideae	Polyphagoideae	Chytridioideae	Entophlyctoideae	Diplophlyctoideae
Representative Genera				
Rhizophydium	Polyphagus	Chytridium	Entophlyctis	Diplophlyctis

It is interesting to speculate upon the possible derivations and interrelations of these five types of thallus development in the monocentric chytrids. (Text fig. 2) Type 1 is assumed to be the most primitive and from it the four other types may be derived. Type 2 is attained by delaying the appearance of the zoosporangium until after the formation of the prosporangium and type 5 is developed in the same way from type 4. Type 4 results if the contents of the encysted zoospore empty into the germ tube and the zoosporangium develops by the enlargement of the germ tube instead of the encysted zoospore. This could have been accomplished if the inside of the substratum penetrated by the germ tube offered a more favorable environment than the outside for the development of the zoosporangium. Here is the connection that does exist between thallus developmental types and the relation of the thallus to its substratum. The relation, however, of the one to the other does not remain constant. Type 3 appears to be intermediate between type 1 and type 4 and may have become established when the enlargement of the germ tube failed to function as a zoosporangium but instead acted as a prosporangium, emptying its contents into the still persistent zoospore cyst and causing the cyst to expand into a zoosporangium.

A classification of the monocentric chytrids based on the types of thallus development can be derived from Sparrow's classification by redefining the families and in part the subfamilies and by rearrangement of the genera. The changes made will be evident from a comparison of the two schemes of classification in Table I. A part of Sparrow's subfamily Phlyctidioideae in the Phlyctidiaceae is merged with the subfamily Rhizidioideae in the Rhizidiaceae. The subfamily Polyphagoideae, as defined by Sparrow, is retained and from it one genus is removed and to it two genera are added. The subfamily Obelidioideae is abandoned, the species included in it by Sparrow being assigned to the subfamily Rhizidioideae. To the Rhizidiaceae is added the Chytridioideae in which are placed *Blyttiomyces* and the species of *Chytridium* and *Phlyctochytrium* having the endo-exogenous type of development. The family Entophlyctaceae n. fam. is created and the family Phlyctidiaceae is abolished. The Entophlyctaceae then is divided into two subfamilies, the Entophlyctoideae Sparrow emend. and Diplophlyctoideae subfam. nov., into which are placed certain genera that are taken chiefly from Sparrow's Phlyctidiaceae and Chytridiaceae. The monocentric operculate genera are assigned to the subfamilies of the Rhizidiaceae and Entophlyctaceae according to the type of thallus development that each possesses, and the family Chytridiaceae is not recognized.

In compliance with the rules of nomenclature the following formal English and Latin descriptions are given for the family Entophlyctaceae and the subfamily Diplophlyctoideae.

Entophlyctaceae fam. nov.[2]

Thallo eucarpico, monocentrico; zoospora encapsulata, quae tubulo germinato extendet, qui vel in zoosporangium vel in prosporangium crescit, a quo zoosporangium incedit; zoosporangium vel operculatum vel inoperculatum; corporibus perdurantibus quibus notibus faciunt vel gamicis vel agamicis duobus thallis conjunctis.

Thallus eucarpic, monocentric; encysted zoospore giving rise to a germ tube that enlarges into either a zoosporangium or a prosporangium from which the zoosporangium develops; zoosporangium operculate or inoperculate; resting body, where known, formed asexually or sexually by fusion of two thalli.

Diplophlyctoideae subfam. nov.

Tubulo germinato quo in prosporangium extendet a quo zoosporangium incedit; zoosporangium vel operculatum vel inoperculatum; corporibus perdurantibus vel gamicis vel agamicis faciunt.

Germ tube giving rise to a prosporangium from which the zoosporangium develops; zoosporangium operculate or inoperculate; resting body sexually or asexually formed.

TABLE I. Sparrow's classification of the eucarpic chytrids occupies the two left-hand columns of the page; the third column on the right is the classification proposed in this paper.

MONOCENTRIC CHYTRIDS

Series: INOPERCULATAE	Series: OPERCULATAE	
Thallus epi- and endobiotic	*Thallus epi- and endobiotic*	*Zoospore cyst functional*
Family: Phlyctidiaceae	Family: Chytridiaceae	Family: Rhizidiaceae
Sporangium epibiotic	Subfamily: Chytridioideae	*Zoospore becomes a sporangium*
Subfamily: Phlyctidioideae	Chytridium	Subfamily: Rhizidioideae
Phlyctidium	Catenochytridium	Rhizoclosmatium
Rhizophydium	Subfamily: Zygorhizidioideae	Siphonaria
Dangeardia	Zygorhizidium	Asterophlyctis
Phlyctochytrium	Subfamily: Macrochytridioideae	Zygorhizidium
Blyttiomyces	Macrochytrium	Nowakowskia
Rhizidiopsis	Subfamily: Endochytrioideae	Solutoparies
Physorhizophidium	Endochytrium	Physorhizophidium
Podochytrium	Nephrochytrium	Podochytrium
Saccomyces		Obelidium
Scherffeliomyces		Rhizidiopsis
Coralliochytrium		Sporophlyctidium
Sporangium endobiotic		Septosperma
Subfamily: Entophlyctoideae		Phlyctidium
Entophlyctis		Dangeardia
Diplophlyctis		Rhizidium
Mitochytridium		Rhizophydium
Rhizosiphon		Rhizophlyctis
Aphanistis		

[2] The Latin diagnoses were prepared by Mr. Harrison A. Nelson.

Thallus interbiotic

Family: Rhizidiaceae

Rhizoids from sporangium
Subfamily: Rhizidioideae
Sporophlyctidium
Rhizidium
Rhizophlyctis

Nowakowskia

Rhizoids from subsporangial apophysis
Subfamily: Obelidioideae
Obelidium
Rhizoclosmatium

Asterophlyctis

Siphonaria

Subfamily: Polyphagoideae

Polyphagus
Sporophlyctis
Endocoenobium

Zoospore becomes a prosporangium
Subfamily: Polyphagoideae
Sporophlyctis
Saccomyces
Rhizosiphon
Polyphagus
Endo- exogenous development
Subfamily: Chytridioideae
Chytridium
Blyttiomyces
Phlyctochytrium
Zoospore cyst nonfunctional
Family: Entophlyctaceae
Germ tube becomes a sporangium
Subfamily: Entophlyctoideae
Coralliochytrium
Scherffeliomyces
Entophlyctis
Mitochytridium
Catenochytridium
Endochytrium
Germ tube becomes a prosporangium
Subfamily: Diplophlyctoideae
Nephrochytrium
Endocoenobium
Diplophlyctis

POLYCENTRIC CHYTRIDS

Series: INOPERCULATAE
Family: Cladochytriaceae

Thallus rhizoidal and septate
Subfamily: Cladochytrioideae
Cladochytrium

Physocladia
Amoebochytrium
Thallus tubular and septate
Subfamily: Catenarioideae
Catenaria
Coenomyces

Series: OPERCULATAE
Family: Megachytriaceae

Nowakowskiella

Septochytrium

Megachytrium

Family: Cladochytriaceae Sparrow em. Whiffen
Septochytrium

Physocladia

Polychytrium
Cladochytrium
Nowakowskiella
Amoebochytrium
Megachytrium
Coenomyces
Catenaria

In the key to the genera of the monocentric chytrids that follows, the assignment of genera to any particular subfamily is in many cases arbitrary. The type of thallus development has not been worked out for many of the chytrid genera and, therefore, these genera are placed in subfamilies on the basis of whatever clues to their development are available. There is no evidence to indicate that the zoosporangium of *Dangeardia* is not formed by the enlargement of the zoospore and so this genus is placed in the Rhizidiaceae, although the resting body appears to be formed from the germ tube rather than from the encysted zoospore. In addition, *Blyttiomyces* and the species of *Chytridium*, which have the endo-exogenous development, represent a deviation from the usual condition in which the resting body has the same origin as that of the zoosporangium; i. e., from the enlargement of either the zoospore or the germ tube. Because of these discrepancies, the present classification is based on the type of development of the zoosporangial stage only. When the resting stages of all of the chytrid genera are known, it may become apparent that there is even less agreement between the ways in which the zoosporangium and the resting body develop than we are now able to recognize. It may then be necessary to modify the present scheme of classification in order to take into account the variations in the types of development of the resting bodies.

Macrochytrium and *Aphanistis* are omitted from the key in this paper because of the impossibility of determining their types of development from the descriptions given. In body form *Macrochytrium* resembles *Cylindrochytrium* or *Catenochytridium* more than any other chytrid genera but there is a possibility that this fungus may be an operculate member of the Blastocladiales. In one of Sorokin's figures of *Aphanistis*, two sporangia appear to be connected by the same septate filament and one is led to think that possibly this genus is polycentric.

Sparrow has pointed out that the genus *Chytridium*, as now defined, is inconsistent in that it includes species with two types of thallus development, the endo-exogenous and the *Rhizophydium* type of development. Since the type species of *Chytridium* apparently has the *Rhizophydium* type of development, it may become imperative that the species with prosporangia be removed from *Chytridium* and segregated in a new genus. The genus *Phlyctochytrium* was originally erected to accommodate the species of *Rhizophydium* with subsporangial swellings but some of the species of *Phlyctochytrium* are supposed to be characterized by the endo-exogenous type of development. That all species of *Phlyctochytrium* have this type of development is extremely doubtful but for the present this genus is placed with *Chytridium* in the Chytridioideae.

KEY TO THE EUCARPIC MONOCENTRIC CHYTRIDS

A. Zoospore cyst functional, enlarging into either a zoosporangium or a prosporangium
Family: **Rhizidiaceae** Sparrow em. Whiffen

B. Zoospore cyst enlarging into a zoosporangium
Subfamily: **Rhizidioideae** Sparrow em. Whiffen

C. Resting body sexually formed by conjugation of two thalli

D. Subsporangial swelling present

E. Zoosporangium spherical in form
Zoospores discharged in an evanescent vesicle .... **Rhizoclosmatium**
Zoospores not discharged in an evanescent vesicle ..... **Siphonaria**

EE. Zoosporangium stellate in form ..... **Asterophlyctis**

DD. Subsporangial swelling absent
Zoospore discharge operculate ..... **Zygorhizidium**
Zoospore discharge inoperculate ..... **Rhizophydium** (in part)

CC. Resting body asexually formed or unknown

F. Zoospore discharge by dissolution of sporangial wall
Zoospores after discharge adhering for some time in a motile flagellate group ..... **Nowakowskia**
Zoospores after discharge separating immediately ..... **Solutoparies**

FF. Zoospore discharge by exit papillae

G. Zoospore discharge operculate ..... **Chytridium** (in part)

GG. Zoospore discharge inoperculate

H. Subsporangial swelling present ..... **Physorhizophidium**

HH. Subsporangial swelling absent

I. Sporangium subtended by a sterile stalk which is cut off by a septum from the sporangium ..... **Podochytrium**

II. Sporangium not subtended by a sterile stalk but the proximal portion of the zoospore cyst (from which the rhizoidal axis arises) expanding less than the distal portion, both portions being fertile and continuous. (See also **III.**)
Apical mucro present on sporangium ..... **Obelidium**
Apical mucro absent from sporangium ..... **Rhizidiopsis**

III. Sporangium not as above; zoospore cyst expanding uniformly and sporangium not subtended by a sterile stalk

J. Zoospore without flagellum ..... **Sporophlyctidium**

JJ. Zoospore with flagellum

K. Rhizoids absent or slightly developed
Resting body stalked ..... **Septosperma**
Resting body not stalked ..... **Phlyctidium**

KK. Rhizoids present and well developed

L. Rhizoids arising from only one point on the sporangial wall

M. Resting body developing from germ tube; zoospore cyst persistent on resting body ..... **Dangeardia**

MM. Resting body developing from encysted zoospore; no persistent zoospore cyst

N. Thallus interbiotic ..... **Rhizidium**

NN. Thallus epi- and endobiotic
Subsporangial swelling present .... **Phlyctochytrium** (in part)
Subsporangial swelling absent ..... **Rhizophydium** (in part)

LL. Rhizoids arising from more than one point on the sporangial wall ..... **Rhizophlyctis**

BB. Zoospore cyst enlarging into a prosporangium (see also **BBB.**)
Subfamily: **Polyphagoideae** Sparrow em. Whiffen

O. Zoospore without flagellum ..... **Sporophlyctis**
OO. Zoospore with flagellum
P. Zoospore discharge by irregular bursting open of sporangial wall **Saccomyces**
PP. Zoospore discharge by exit papillae or tubes
Nutrient absorbing system non-rhizoidal, consisting usually of two broad, unbranched, hypha-like structures; resting body asexually formed **Rhizosiphon**
Nutrient absorbing system rhizoidal and branched; resting body sexually formed ..... **Polyphagus**
BBB. Germ tube giving rise to a prosporangium the contents of which contribute to the subsequent enlargement of the zoospore cyst into a zoosporangium Subfamily: **Chytridioideae** Sparrow em. Whiffen
Q. Zoospore discharge operculate ..... **Chytridium** (in part)
QQ. Zoospore discharge inoperculate
Zoosporangium with an apiculus that is developed from a thickened portion of the zoospore cyst ..... **Blyttiomyces**
Zoosporangium without an apiculus that is so developed **Phlyctochytrium** (in part)
AA. Zoospore cyst not enlarging into a zoosporangium or a prosporangium; germ tube enlarging into a zoosporangium or prosporangium Family: **Entophlyctaceae** Whiffen
R. Germ tube enlarging into a zoosporangium Subfamily: **Entophlyctoideae** Sparrow em. Whiffen
S. Zoospore discharge inoperculate
T. Empty zoospore cyst persistent at maturity of thallus
Subsporangial swelling present; rhizoidal system consisting of short digitations ..... **Coralliochytrium**
Subsporangial swelling absent; rhizoidal system consisting of slender branches ..... **Scherffeliomyces**
TT. Empty zoospore cyst not persistent at maturity of thallus
Sporangium sub-spherical to spherical in form ..... **Entophlyctis**
Sporangium a branched or unbranched elongated tube .. **Mitochytridium**
SS. Zoospore discharge operculate
U. Rhizoids constricted into catenulate segments near the base of the sporangium
Sporangium sub-spherical in form ..... **Catenochytridium**
Sporangium cylindrical in form ..... **Cylindrochytridium**
UU. Rhizoids not so constricted ..... **Endochytrium**
RR. Germ tube enlarging into a prosporangium Subfamily: **Diplophlyctoideae** Whiffen
V. Zoospore discharge operculate ..... **Nephrochytrium**
VV. Zoospore discharge inoperculate
Zoospore cyst persistent at maturity of thallus ..... **Endocoenobium**
Zoospore cyst not persistent at maturity of thallus ..... **Diplophlyctis**

If the eucarpic polycentric chytrids are not to be separated into operculate and inoperculate families, Sparrow's Megachytriaceae and Cladochytriaceae, respectively, the question arises as to whether or not the polycentric chytrids constitute more than one family. At present it seems best to retain the nine polycentric genera in one family, the Cladochytriaceae.

It is possible, however, to recognize three intergrading types of thallus structure among the polycentric chytrids. The first type, represented by *Septochytrium variabile* Berdan, suggests a possible transition from such a monocentric chytrid as *Endochytrium* to the polycentric form. Whereas

in *Endochytrium* the rhizoids are without nuclei, in *Septochytrium* nucleated centers of growth are established by migration of nuclei from the incipient primary sporangium into the rhizoids where there appear swellings which develop into secondary sporangia. *Catenaria*, *Coenomyces*, and *Megachytrium* are representatives of the second type in which the thallus is broadly tubular and often septate. Karling (1939) has put *Coenomyces* and *Megachytrium* in a separate family, Myceliochytriaceae. In the third type, to which belong *Cladochytrium*, *Nowakowskiella*, *Physocladia*, *Amoebochytrium*, and *Polychytrium*, the thallus is much branched, tenuous, with numerous rhizoids and irregular swellings.

The fate of the encysted zoospore is not known for each polycentric genus. In *Septochytrium variabile* (Berdan, 1941) and *Cladochytrium hyalinum* (Berdan, 1942) the contents of the encysted zoospore empty into the developing rhizomycelium and the zoospore itself takes no further part in the development of the thallus. It is possible that the encysted zoospore is also non-functional in all of the other polycentric genera except *Amoebochytrium* in which the zoospore sometimes gives rise to a zoosporangium.

SUMMARY

The relative values of operculation, relation of the thallus to its substratum, and the types of thallus development in deriving a classification of the Chytridiales are discussed. It is argued that operculation or the lack of it is of minor importance and that the positional relationship of the chytrid thallus to its substratum, with the exception of the obligate parasite, is too variable to be a reliable taxonomic criterion. Five types of thallus development are described. It is proposed that the genera of the monocentric chytrids be grouped into two families on the basis of whether the zoosporangium develops from the encysted zoospore (Rhizidiaceae) or from the germ tube of the zoospore (Entophlyctaceae). The Rhizidiaceae is divided into the subfamilies, Rhizidioideae, Polyphagoideae, and Chytridioideae; and Entophlyctaceae into the Entophlyctoideae and Diplophlyctoideae, each of the subfamilies representing a different type of thallus development. A key to the genera of the monocentric chytrids is provided. The genera of the polycentric chytrids are surveyed and it is suggested that for the present they be retained in one family, the Cladochytriaceae.

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STUDIES IN THE GENUS HELOTIUM, IV SOME MISCELLANEOUS SPECIES[1]

W. Lawrence White[2]

In this series of papers such familiar names as *Helotium citrinum*, *H. cyathoideum*, *H. fructigenum*, *H. herbarum*, and *H. virgultorum*, and the species to which they apply, have been avoided, while *H. epiphyllum* and *H. scutula* have been subjected to only preliminary treatment. These names have in common the fact that they are pre-Friesian, represent species which have fairly large apothecia, are of widespread distribution, and are of common occurrence. They are the species most frequently found by the collector. They have been recorded many times, but in no case have they received detailed or modern taxonomic treatment. The problems they offer are intricate and difficult and not susceptible to quick solution. These problems are being disentangled gradually and it is hoped that treatments of at least some of the pre-Friesian species may be made ready for publication in the near future. In the meantime the present installment comprises a sorting out of a miscellany of eight species, which have been under consideration for the past three or more years, and for which the accumulated taxonomic data appear to be as complete as they can be made at the present time. They are species occurring in either Europe or North America or which are common to both continents. Each is represented by one to several collections providing enough material to permit the preparation of what should prove to be fairly adequate descriptions: none of them ranks among the more common or so-called better known members of the genus.

A complete and critical bibliography is attempted for all the species except no. 5, *H. albidum*. Microscopic observations are based on material mounted in KOH-phloxine. Drawings showing structure are made from freehand sections. Technical color terms are those of Ridgway. Herbarium abbreviations are those of Lanjouw to which extra letters are added when needed to designate subdivisions or private collections: CU-P = Plant Pathology Herbarium at Cornell University; CU-PD = its Durand Herbarium; CU-PF = its Fairman Herbarium; FH = Farlow Herbarium; FH-E = its Ellis Herbarium; NY = New York Botanical Garden Herbarium; NY-E = its Ellis Collection; NY-M = its Massee

[1] Contribution from the Laboratories of Cryptogamic Botany and the Farlow Herbarium, Harvard University, no. 224.

[2] The writer, now on leave to the Chemical Warfare Service Development Laboratory, Massachusetts Institute of Technology, wishes to express his thanks to Dr. Rolf Singer of the Farlow Herbarium for preparing the Latin diagnoses, and to the several individuals who have contributed specimens, in particular to Professor H. M. Fitzpatrick and Dr. Fred J. Seaver for making available important historic material under their care at Cornell University and the New York Botanical Garden respectively, and to Professor H. H. Whetzel of Cornell University for supplying so many of the more recent collections.

Collection; OTB = Botany Department Herbarium, Central Experimental Farm, Ottawa; US = Pathology and Mycology Collections, United States Department of Agriculture.

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FIGURES 1–5.

Apothecia scattered, not numerous, sessile, attached by a broad central portion, free at the margin, when fresh 0.8–1.2 mm. diam., rarely reaching 1.7 mm., bright dilute yellow, concolorous on all parts, of medium thickness, plane to convex, strongly convex with maximum water content, drying fairly thin, plane to saucer-shaped; **receptacle** always smooth, on drying remaining yellow or turning slightly whitish; **hymenium** drying firmly waxy and opaque, becoming deep golden yellow, varying among "Cadmium Yellow," "Light Orange Yellow," "Deep Chrome," or "Ochraceous Buff," sometimes in very old herbarium specimens deepening to "Sanford's Brown"; **margin** lying close to the substratum in fresh material, on drying turning upward, finally usually slightly elevated, smooth, regular; **in section** 170–200 μ thick from substratum to hymenial surface, colorless or practically so; *medullary region* prosenchymatous, rather open, the hyphae thin-walled, 4–6 μ diam., rarely reaching 10 μ; *ectal layer* thick and well differentiated, pseudoparenchymatous, the cells thin-walled, 4–10 μ diam., isodiametric, angular, or more or less elongate in direction from center to outside, not crowded; **paraphyses** mostly once-forked at or below the middle, a few of them simple or twice-forked, the apices clavate-enlarged, 2–3.5 μ diam.; **asci** originating from croziers, clavate-cylindric, 40–55 x 6–7 μ; **ascospores** biseriate in the upper part of the ascus, uniseriate below, elongate, straight to slightly curved or irregular, thickest at or above the middle, more or less obtusely pointed at the ends, 7–11 x 2–2.5 μ, 1-celled, or in some specimens a few 2-celled, the content homogeneous, lacking oil globules.

Habitat: On dead culms and leaves of grasses and sedges, perhaps also on other monocotyledonous plants; most frequent on wooded hillsides and always appearing well down among the basal portions of the plants where the parts are constantly moist, only rarely found on plants growing in swamps or other habitats:

Distribution and specimens examined: NORTH AMERICA. **Massachusetts:** On *Carex* sp., Wakefield, May 2, 1942, *D. H. Linder & W. L. White* (FH). — **New York:** Lyndonville, Apr. 1906, *C. E. Fairman*, as *Helotium citrinulum* Karst., det. Rehm, reported by Fairman in 1910 (l. c.) (CU-PF). — On *Phleum pratense* L., Forest Home, Ithaca, May 14, 1907, *E. J. Durand & H. H. Whetzel* (CU-PD *5181*). — On *Carex plantaginea* Lam., Labrador Lake, May 5, 1936, *W. L. White* (CU-P *25189*, FH, NY, OTB). —Additional collections from same locality and substratum: May 16, 1936, *White* (FH); May 9, 1937, *White* (FH); May 23, 1937, *White* (FH). — On *Carex* sp. (not *plantaginea*), Labrador Lake, May 23, 1937, *White* (FH). — On *Carex* sp., Arnot Forest, near Ithaca, May 25, 1937, *White 2953, 2954* (FH). — On grass, Arnot Forest, May 25, 1937, *White* (CU-P *25823*, FH). — **Ontario:** On *Maianthemum canadense* Desf. (according to the collector), Bear Island, L. Temagami, May 29, 1936, *J. W. Groves*, Univ. Toronto Crypt. Herb. *17620*, comm. H. S. Jackson (FH). — On *Carex* sp., May 1905, *F. J. Seaver*, Rehm Ascom. *1634*, type of *Helotium citrinulum* var. *Seaveri* (CU-P, FH). — On *Carex* sp., June 8, 1905 (CU-PD *502*, NY-M). — EUROPE: **Finland:** On *Carex vesicaria* L., Mustiala, Finl. Fungi comm. Karsten, authentic material of *Helotium citrinulum* (NY). Karsten (1871) noted that he had encountered the species several times on gramineus hosts about Helsingfors and Mustiala in April and May. — **? Denmark:** From the dubious report of Lind (1913), which assumes that *H. album* Schum., unknown since 1801 may be identical with Karsten's species. — **Germany:** Reported by Rehm (1893) on grasses and by Schröter (1893) on grasses and on *Carex vaginata* Tausch. — **? Czechoslovakia:** Reported by Velenovsky on *Phragmites* sp. Description and illustrations poor. — **France:** Based on report by Saccardo (1882 and 1883) of its occurrence on *Phragmites communis* Trin. Illustrations good. — **England:** "Near base of culms of *Dactylus glomerata*." Shere, Surrey, type of *Helotium flexuosum* (NY-M).

The species is distinguished by its golden yellow, broadly sessile, and rather spreading apothecia, and by its occurrence on dead grasses and sedges for a short period in the spring of the year. In aspect the apothecia are similar to those of *Helotium callorioides* Rehm as illustrated by Boudier on his plate *444* sub *Calycella callorioides* (Rehm) Boud. The apothecia of *Helotium citrinulum*, however, are not lobed as Boudier illustrates those of *H. callorioides*, and they are attached to the substratum by a broader basal portion than is indicated in Boudier's illustration, though it is not always as broad as I have illustrated it in the accompanying diagram (Fig. 1). These apparent differences are at best minor, and a perusal of Rehm's original description of *H. callorioides* (Hedwigia **21** (7): 98. 1882), together with that of Boudier, indicates that the lobed condition is probably not normal for that species and that the apothecia are entirely sessile. As another difference, also of probable minor significance, may be mentioned the fact that the material thus far referred to *H. citrinulum* has been on monocotyledonous substrata, while Rehm's material of *H. callorioides* was on the ranunculaceous *Aconitum variegatum* and that of Boudier on *A. napellus*. No ma-

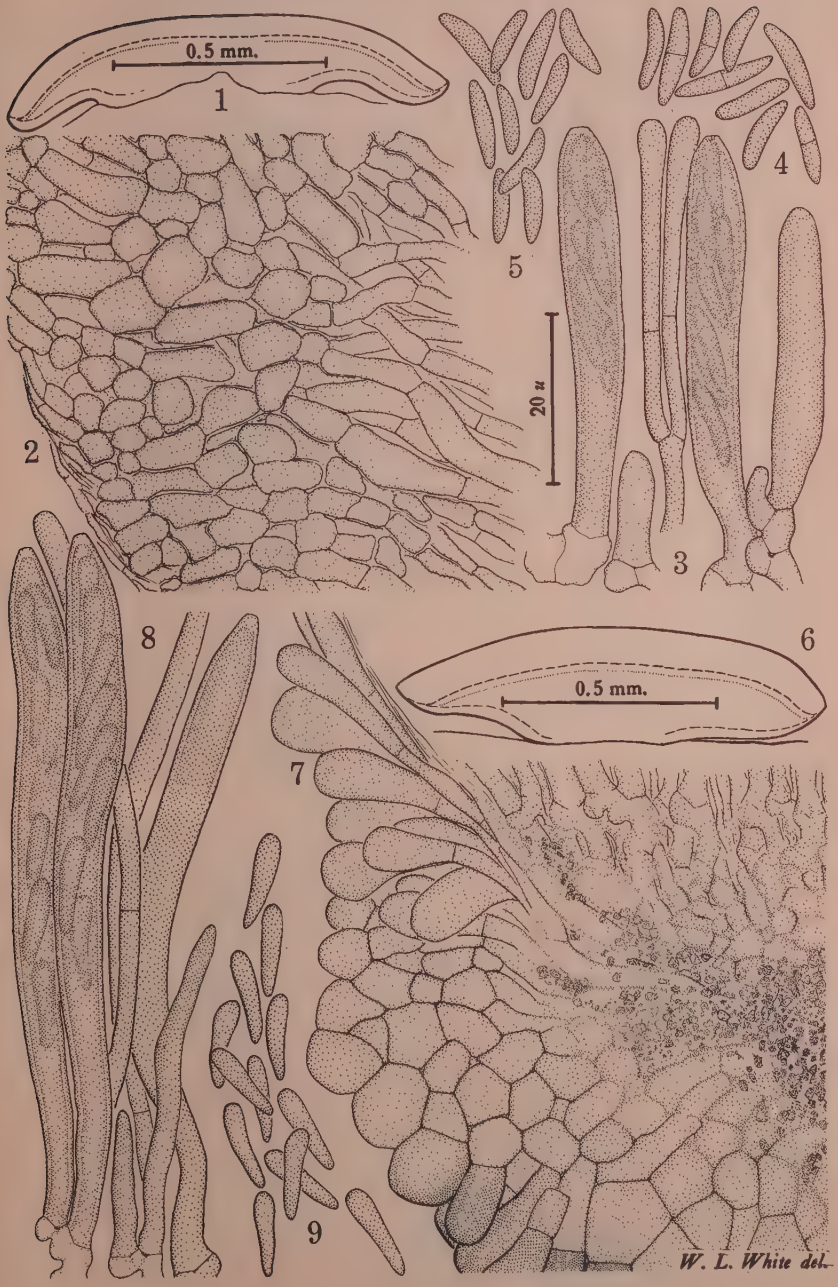
terial of *H. callorioides* is available for examination. Karsten's specific epithet, *H. citrinulum*, has priority in case the two species should later prove to be synonymous.

The several collections here presented as *Helotium citrinulum* have been carefully studied and they indicate a species of rather uniform characters. The Karsten and Massee specimens show a hymenium of somewhat deeper color than the others, but this may be due, in part at least, to age; at any rate, the degree of coloring in the yellow species of *Helotium* has proven entirely unreliable as a taxonomic character. The specimens exhibit little or no variation in the structure of the apothecium (Fig. 2). They further show remarkable uniformity of the various hymenial elements: all have paraphyses that are predominantly once-branched at or near the middle (Fig. 3) but occasionally simple or twice-forked, and which are noticeably clavate-enlarged at the immediate apex. All have asci (Fig. 3) originating from rather poorly developed croziers which do not stain well, and appear to be without content, and thus are difficult to discern clearly under the microscope. The spores (Fig. 4–5) are characteristically variable within each collection but show no noticeable variation among the several specimens, with the exception that about half those of the Finland (Karst.) specimen (Fig. 4) examined are septate, as is also true of the Ontario specimen. Septate spores have not been seen in any of the other collections. The spores, whether from fresh or herbarium material, never contain oil globules or granular content. All specimens have been taken during the spring of the year. That the species actually is limited in apothecial production to a brief period at this season is attested by the fact that repeated search at Labrador Lake, N. Y., where it was known to produce apothecia on *Carex plantaginea* during May always failed to reveal any fruit bodies after the latter part of that month.

Mass ascospore cultures were made from CU-P *25189*. The ascospores germinated readily on potato dextrose agar at room temperature and did not become septate in the process. A rather rapidly growing white mycelium developed. In old cultures the mycelium and also the agar became decidedly yellow. The cultures were carried for a year during which period, transfers were subjected to various conditions of temperature and humidity, but no fruit bodies, stromata, or spores of any kind ever developed.

Fig. 1–5, Helotium citrinulum: 1, Diagrammatic representation of section through an apothecium, × 74 (CU-P *25189*); **2,** Section through the ectal excipulum at base of hymenium showing structure. From specimen taken at Wakefield, Mass., × 1290 (FH); **3,** Asci and paraphyses. From Karsten specimen as *H. citrinulum*, × 1290 (NY); **4,** Ascospores from same specimen, × 1290; **5,** Ascospores from type of *H. flexuosum*, × 1290 (NY-M).

Fig. 6–9, Pezizella culmigena, all from **type** (FH): **6,** Diagrammatic representation of section through an apothecium, × 74; **7,** Section showing structure of disc tissue, × 1290; **8,** Asci and paraphyses, × 1290; **9,** Ascospores, × 1290.



FIGURES 1–9

2. **Pezizella culmigena** Sacc., Ann. Myc. **12**: 292. 1914. — Sacc., Syll. Fung. **24**[2]: 1189. 1928.

FIGURES 6–9.

Apothecia subgregarious, rather numerous, sessile, attached by a broad central portion or at least appearing so, free at the margin, yellow, about 0.6–1.1 mm. diam. when dry, not perceptibly larger when moistened, when dry fairly thin, plane to saucer-shaped, when moistened somewhat thicker, cushion-shaped; **receptacle** smooth, when dry turned slightly off the substratum at the margin, slightly olive-brown toward the base, pale yellow above, "Chamois" to "Honey Yellow," on moistening remaining nearly the same color, lying closely adjacent the substrate; **margin** circular, even, rarely slightly lobed or angular, obtuse, rather thin, when dry even with the hymenium or slightly elevated, when moistened directed outward and downward against the substratum, concolorous with upper part of receptacle; **hymenium** when dry plane, waxy, concolorous with receptacle and margin, becoming slightly convex on moistening; **in section** 170–200 μ thick from substrate to hymenial surface; *medullary region* very compact, of indeterminate structure, containing a large amount of crystalline material; *ectal layer* distinct, well differentiated, about 30 μ thick at the base, somewhat thinner toward the margin, composed of compact, more or less angular, thin-walled cells 9–12 μ diam., colorless except for those in the outer layer which in the basal region of the apothecium are brown and have walls slightly thickened, those at the margin of the disc clavate; **paraphyses** simple, colorless, thin-walled, non-staining, slightly clavate at the apex, 3–4 μ diam.; **asci** originating from croziers, narrow, clavate, 65–68 x 6–7 μ; **ascospores** biseriate in the upper part of the ascus, uniseriate below, cuneate, rounded above, tapering to an obtuse point below, straight or slightly curved, the sides sometimes slightly irregular in outline, 8.5–10 x 2.4–2.6 μ, 1-celled, lacking oil globules.

Known only from the **type**: On decaying culms of *Phragmites communis* Trin., Weisskirchen, Mahren, Bohemia, May 1914, *F. Petrak* (FH).

Saccardo in his original description indicates that this species is close to *Helotium citrinulum*. Superficially the apothecia of the type (Fig. 6) differ but slightly from those of *H. citrinulum* (Fig. 1) in being less brightly colored than most specimens of the latter and in being slightly grayish on the lower portion of the receptacle. Microscopically the species is distinct from *H. citrinulum* in its wedge-shaped spores (Fig. 9), long and narrow asci (Fig. 8) and different structure (Fig. 7). The hyphae of the medullary excipulum do not stain well, the walls are thin and appear to become confluent, and the tissue contains a large amount of obscuring mineral matter (Fig. 7). It is not certain whether the structure is fundamentally prosenchymatous or pseudoparenchymatous. In contrast, the corresponding region in *H. citrinulum* (Fig. 2) is rather loose and open and the hyphae are distinct. Also in *Pezizella culmigena* (Fig. 7) the ectal layer is more clearly defined, more rind-like, and more compact than in *Helotium citrinulum*, and the outer layer of cells in the basal

portion of the apothecium is brown, whereas in *H. citrinulum* the entire tissue is practically colorless. It is possible that the two species are less closely allied than their superficial resemblances would at first indicate.

3. **Helotium midlandensis** sp. nov.

FIGURES 10–13.

Apotheciis sparsis vel subgregariis, plerumque solitariis, rarius trinis vel octonis, stipitatis, flavis vel aurantiacis, 0.3–0.7 mm. in diam. et eaque altitudine; stipite sat gracili, cylindrico, levi, pallide flavo; disco apiriente depressione minuta citoque applanata, subcarnoso, remanente solido in siccis; receptaculo stipiti concolori, in siccis minute-ericeo-striolato de margine usque ad apicem stipitis, levi in humidis; hymenio plano vel patelliformi, rarius leviter convexo, flavo vel aurantiaco; margine levi, obtuso, circulari vel angulato ex pressione marginum aggregatorum attingentium; paraphysibus, simplicibus, interdum unum ramum prope basim gerentibus, cylindraceis, 3–5 septatis, 2.4–3.2 μ in diam.; ascis e "croziers" natis, clavatis, 45–65 x 6.5–6 μ; ascosporis biseriatim vel subbiseriatim dispositis, unicellulatis, plus minusve ovoideis, 7–10x2.6–3.2 μ.

Apothecia known only from dried specimens, scattered to subgregarious, usually solitary, more rarely in clusters of three to eight, stipitate, in general aspect yellow or orange-yellow, 0.3–0.7 mm. across the disc and of about the same height; **stipe** rather slender, cylindric or essentially so, smooth, pale yellow; **disc** opening by a minute depression, very soon plane, subfleshy, retaining its original fullness on drying; **receptacle** concolorous with stipe, when dry showing fine, silky superficial striae radiating from top of stipe toward margin, smooth when moistened; **hymenium** plane to patelliform, more rarely slightly convex, yellow or orange-yellow; **margin** smooth, obtuse, circular, or when crowded becoming angular from mutual pressure; **in section:** *stipe* about 180 μ thick, very compact, composed of narrow, parallel hyphae about 3 μ diam. with narrow lumen and thickened, confluent walls, those near the surface turning outward and ending in a thin indefinite zone 12–18 μ thick and composed of isodiametric cells 3–6 μ diam.; *medullary region* of disc fairly compact, of thin-walled hyphae 2.5–3.5 μ, much branched and interwoven; *ectal layer* compact, 40–50 μ thick, composed of narrow, parallel hyphae 3–4.5 μ diam., except at or near the surface where a few are of somewhat larger diameter and the cells shorter; *subhymenium* not differentiated from the medullary layer; **paraphyses** simple or occasionally once-branched near the base, cylindric, 3–5-septate, 2.4–3.2 μ diam.; **asci** originating from croziers, clavate, 45–65 x 6.5–7 μ; **ascospores** biseriate or subbiseriate, 1-celled, irregularly obovoid, 7–10 x 2.6–3.2 μ.

Habitat: One specimen (Iowa, *Grumbein*) on petioles and larger leaf veins of old leaves of *Quercus* sp.; all others on old pods of *Gleditsia triacanthos* L.

Distribution and specimens examined: **Ohio:** *Morgan 801*, reported incorrectly (Morgan, Journ. Mycol. **8:** 184. 1902; Seym., Host Index, p. 416. 1929) as *Helotium discretum* Karst. (NY-E). — **Iowa:** Homestead, Sept. 26, 1931, *G. W. Martin 5186*, **type** (FH). — Hills, Dec. 3, 1933, *G. W. Martin 5191* (FH). — (With *Typhula juncea*), North Liberty, Oct. 4, 1941, *M. L. Grumbein* (FH). — **Kansas:** Lawrence, 1890, *W. C. Stevens 59*, incorrectly labeled *Helotium herbarum* (NY-E).

This species has much the aspect of *Helotium immutabile* Fuckel and other members of the *H. epiphyllum* group (cf. White, Farlowia **1**: 137, 139–147. 1943) to which it belongs. It is distinguished among these species by its small size, the comparatively slight parenchymatous differentiation of the ectal layer of the disc, small asci, and small egg-shaped spores. Compare the following species.

4. **Helotium erraticum** sp. nov.

FIGURES 14–18.

Apotheciis paucis, sparsis vel subgregariis, stipitatis, albis vel cremeo-flavis, usque ad 2.5 mm. latis et 1 mm. altis, siccando flavescentibus, cartilagineis; stipite crasso, plus minusve cylindraceo, levissimo, albo-hyalino, lutescente siccando; disco depressione minuta aperto, mox applanato, carnoso, levi, albo, siccando lutescente vel rubescente; hymenio albo, plano, siccando lutescente vel rubescente, opaco vel plus minusve pellucido, cupuliformi; margine levi, obtuso. — Stipite consistente ex hyphis parallelis, densis, 2.5–5 μ crassis, tenuitunicatis, et ad basin et secundum superficiem expositam brevioribus et 4–10 μ crassis, membranis crassiusculis praeditis; excipulo ectali disci indefinito, admodum compacto, ad basin crasso, marginem versus tenuiore, ca. 40–50 μ crasso in parte media inter basin et marginem; regione medullari minus compacta; subhymenio vix distincto a medulla; paraphysibus longis, rectis, simplicibus vel rarissime semel furcatis prope basin, ad apicem clavatis, ascos longitudine paululum superantibus, 2.8–3.5 μ crassis; ascis e "croziers" natis, clavatis, 90–120 x 9–11.5 μ; ascosporis biseriatim dispositis, subtus autem unam tantum seriem formantibus, oblongis vel obovoideis, subcurvatis vel unum ad latus applanatis atque utrinque subattenuatis, interdum plus minusve crepiduliformibus, praecipue cum membrana asci iam compressae sunt, uni-cellularibus, 11–17 x 3.5–4 μ, guttulis olei globulosis conspicuis binis apicalibus instructis. Habitatio: Ad folia putridissima arborum frondosarum.

Apothecia few, scattered or rarely subgregarious, stipitate; when fresh, white to creamy yellow, up to 2.5 mm. diameter and 1 mm. high, more often 0.5–1.0 mm. across the disc, and 0.6–0.8 mm. high; in drying, contracting slightly, becoming yellow or dull reddish yellow, "Chamois" to "Cinnamon-Rufous" or "Orange-Cinnamon," cartilaginous and of more or less the same color and consistency throughout; **stipe** stout, cylindric or essentially so, entirely smooth, hyaline-white when fresh, drying translucent-yellow; **disc** opening by a minute depression, soon plane, fleshy, contracting slightly on drying, more or less saucer-shaped, remaining thick; **receptacle** smooth, when fresh white, drying translucent-yellow below, similar toward the margin or of a brighter and more opaque yellow, or sometimes uniformly yellow or reddish; **hymenium** when fresh white or nearly so, plane, on drying becoming bright yellow

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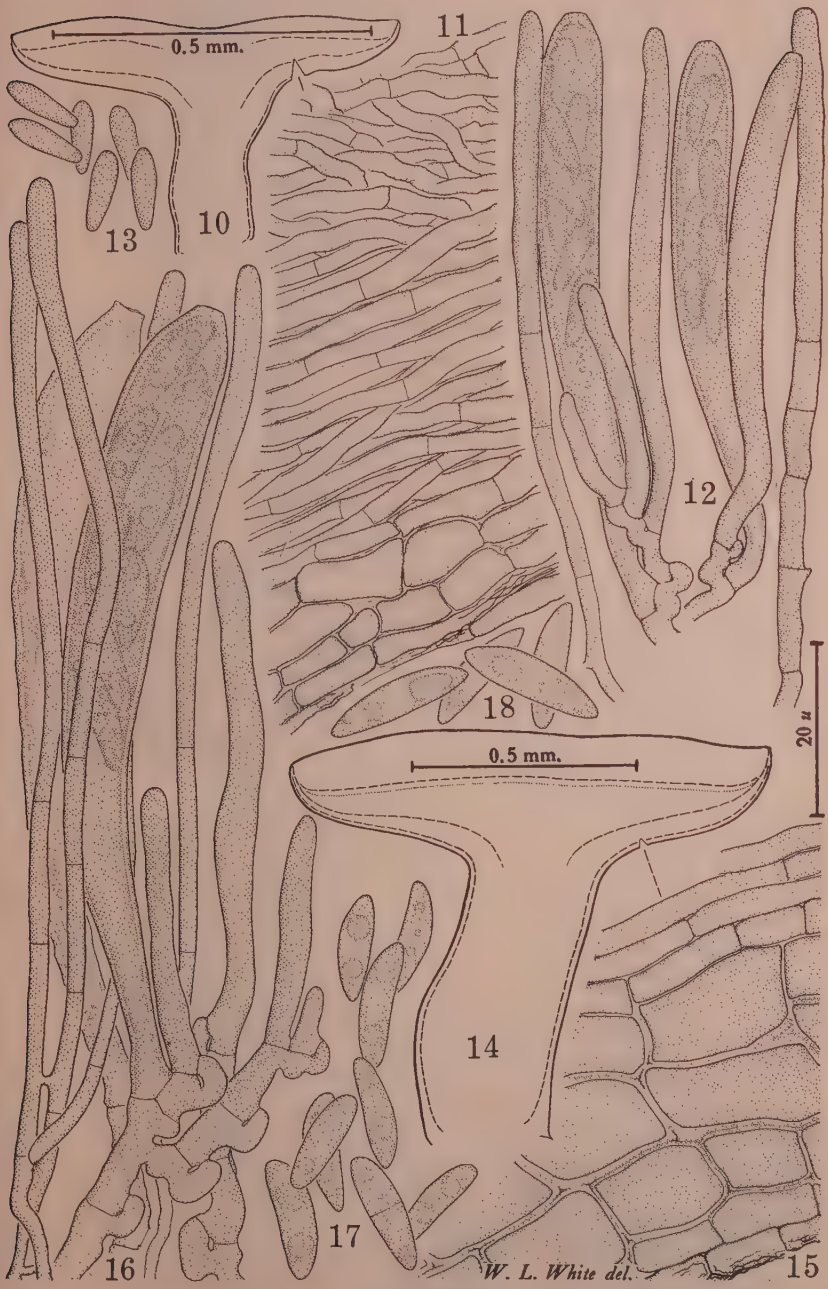
Fig. 10–13, Helotium midlandensis: 10, Diagrammatic representation of section through apothecium, × 110, from type (FH); **11,** Section through ectal excipulum, *Martin 5191*, × 1290 (FH); **12,** Asci and paraphyses, from type, × 1290 (FH); **13,** Ascospores from type, × 1290 (FH).

Fig. 14–18, Helotium erraticum: 14, Diagrammatic representation of section through apothecium, from type, × 78 (FH); **15,** Section through ectal excipulum, from CU-P *27850* (FH); **16,** Asci and paraphyses, from CU-P *29658*, × 1290 (FH); **17,** Ascospores, from CU-P *29658*, × 1290 (FH); **18,** Ascospores, from TRT *17611*, × 1290 (FH).



FIGURES 10–18

to reddish, opaque or more or less translucent, saucer-shaped; **margin** even, obtuse, drying slightly elevated and very slightly undulate or wrinkled; **in section:** *stipe* composed of very compact, parallel hyphae, 2.5–5 μ diameter, thin-walled except at the base and along the exposed surface where the cells are shorter and thicker, 4–10 μ diameter, with walls slightly thickened and confluent; *ectal excipulum* of disc indefinite, very compact, thick at the base, thinner toward the margin, about 40–50 μ thick half way between base and margin, the hyphae similar to those of the stipe, the outermost ones similarly somewhat larger in diameter and with walls slightly thickened, forming a thin rind layer extending nearly to the margin; *medullary region* slightly less compact, of thin-walled hyphae 2.5–5 μ diam., much branched and interwoven in all directions; *subhymenium* scarcely differentiated from the medullary region; *paraphyses* long, straight, unbranched, or very rarely once-branched close to the base, clavate at the apex, extending somewhat beyond the asci, 2.8–3.5 μ diam.; **asci** originating from croziers, clavate, 90–120 x 9–11.5 μ; **ascospores** biseriate above, uniseriate below, oblong or obovoid, slightly curved or flattened on one side, slightly pointed toward the ends, sometimes appearing more or less slipper-shaped especially when crowded in the ascus, 1-celled, 11–17 x 3.5–4 μ, with a conspicuous and rather large oil globule in each end.

Habitat: On much decayed leaves of various frondose trees (as listed below); one collection on old pods of *Robinia Pseudoacacia* L.

Distribution and specimens examined: **Quebec:** On *Acer* sp., *Populus* sp., & sp. indet., Duchesnay, Aug. 25, 1938, *H. H. Whetzel & T. Sproston,* previously reported (Mycologia **31:** 730. 1939) as *Helotium phyllophilum* and (White, Farlowia **1:** 141, 159. 1943) as *H. epiphyllum* (CU-P *27850,* FH). — Duchesnay, Aug. 26, 1938, *R. F. Cain 11154,* reported (Mycologia, l. c.) as *H. immutabile* and (White, l. c., p. 141, 147) as *H. epiphyllum,* spec. comm. H. S. Jackson (FH). — **New York:** On *Acer* sp., Coy Glen, near Ithaca, Oct. 3, 1938, *H. H. Whetzel & W. L. White 3416* (FH). — On *Acer* sp. ?, Coy Glen, Oct. 3, 1938, *Whetzel & White 3421,* **type** (FH). — On *Amelanchier* sp., *Hamamelis* sp., & *Ulmus* sp., Malloryville, near Ithaca, Oct. 18, 1941, *H. H. Whetzel & J. Niederhauser* (CU-P *29658,* FH). — On pods of *Robinia Pseudoacacia* L., Newfield Gorge, near Ithaca, Oct. 26, 1941, *H. H. Whetzel & T. Sproston* (CU-P *29666,* FH). — **Ontario:** On *Acer* sp., Brewer Lake, Algonquin Park, Sept. 5, 1939, *R. F. Cain,* comm. Jackson, TRT *17611* (FH).

This is another member of the *Helotium epiphyllum* group and must be cautiously separated from such species as *H. epiphyllum, H. immutabile, H. carpinicola,* and *H. midlandensis.* These species appear to be distinct and taxonomically satisfactory, but may be somewhat difficult for one who has had no experience with them. They cannot be separated with any degree of certainty macroscopically, but under the microscope are distinct on a number of characters, the final and most important being spore size and shape.

5. **Helotium albidum** (Rob. ex Desm.) Pat., Tab. Anal. Fung. **4:** 173, *fig. 382a–d.* 1885.

Peziza albida Rob. ex Desm., Ann. Sci. Nat. 3: **16:** 323. 1851.
Helotium scutula (Pers. ex Fr.) Karst. var. *albidum* (Rob. ex Desm.) Karst., Myc. Fenn. I, Bidr. Känn. Finl. Nat. Folk **19:** 112. 1871.

Phialea albida (Rob. ex Desm.) Gill., Champ. France, Discom., p. 105. 1879–1883.
Hymenoscypha albida (Rob. ex Desm.) Phill., Man. Brit. Discom., p. 138. 1887.

FIGURES 19–24.

Apothecia arising from black areas 1-several cm. long on the leaf petiole, 6–20 on each such area, scattered to subgregarious, stipitate, in the dried condition up to about 1.2 mm. high and 1.5 mm. across the disc, the larger ones expanding to 2 mm. when moistened, in the fresh condition creamy white or ivory white (Desm.) or with maximum moisture content more dilute in color, drying with stipe and outside of disc essentially concolorous, "Cinnamon" or "Pinkish Cinnamon," and the hymenium "Orange-Cinnamon"; **stipe** cylindric, slender but not delicate, minutely scabrous when dry; disc subfleshy, spreading, saucer-shaped when dry; **receptacle** when dry finely and closely lined with superficial radiating striae; **margin** even, when dry conspicuously elevated above the hymenium; **hymenium** drying firmly waxy; **in section:** *stipe* composed of a broad central core, hyaline, of thin-walled hyphae about 4–6 μ diam., and a thin, yellowish, cortical layer 4–5 cells thick and composed of short rectangular cells; *medullary region* of disc compact, composed of hyphae similar to those making up the central core of the stipe; *hypothecium* not noticeably differentiated; *ectal layer* not sharply distinguished, consisting of a zone about five cells thick made up of large hyphae 8–10 μ or rarely up to 15 μ diam., over which is a thin external covering of narrow more or less crushed or collapsed hyphae of smaller diameter; **paraphyses** simple, usually 3-septate, slightly enlarged toward the apex, about 3 μ diam.; **asci** clavate-cylindric, not originating from croziers, 90–100 x 10–12 μ; **ascospores** uniseriate below, biseriate above, 1-celled, 13–17 x 4–5 μ, rounded above, very slightly tapering toward the lower end, slightly curved or flattened on one side, obtuse-pointed below, the content granular.

On fallen, decaying petioles of *Fraxinus excelsior* in France. Known with certainty only from the material of Desmazières: Pl. Crypt. Fr., ed. 1, *2004;* ed. 2, *1604* (FH).

This is a member of the *Helotium scutula* complex in which many forms, varieties and species have been described. It is being allowed to stand as distinct from *H. scutula* or *H. caudatum*, the former on herbaceous stems and the latter on leaves. It is more robust than *H. caudatum* and differs from both it and *H. scutula* in having spores which are smaller in size and more obtuse at the lower end. If it proves to be confined to *Fraxinus* petioles where it causes blackening, and if spore and other characters are constant, then it may be maintained as a species. The references listed above are only those pertinent to the synonymy. There are many European records, but they are based largely upon specimens better referred to *H. caudatum* or *H. scutula*.

6. **Helotium scutula** (Pers. ex Fr.) Karst. var. **fucatum** (Phill.) in Rehm *in* Rabenh. Krypt.-Fl. **1**[3]: 793. 1893. — Massee, Brit. Fung.-Fl. **4**: 254. 1895. — Boud., Hist. Classif. Discom. Europe, p. 114. 1907.

Peziza fucata Cooke & Phill.; Cooke, *nom. nud.*, Grevillea **4**: 132, *pl. 65, fig. 300.* 1876.

Hymenoscypha scutula (Pers. ex Fr.) Phill. var. *fucata* Phill., Man. Brit. Discom., p. 137. 1887.

Phialea scutula (Pers. ex Fr.) Gill. var. *fucata* (Phill.) Sacc., Syll. Fung. **8**: 266. 1889. — Seaver, Bull. Lab. Nat. Hist. State Univ. Iowa **6**[2]: 101. [Oct. 1911], spec. & descr. excluded. — Oud., Enum. Syst. Fung. **2**: 1004. 1920. — Seym., Host Index, p. 292. 1929, based on Seaver's report (l.c.).

FIGURES 25–30.

Apothecia scattered to subgregarious, fairly numerous, stipitate, hyaline-white when fresh, or sometimes yellowish-stained, 1–3 mm. high, up to 2.8 mm. across the disc though usually smaller, drying yellowish ochraceous, all parts approximately concolorous in both fresh and dried conditions, the disc contracting somewhat in drying, usually not over 1 mm. diam. in herbarium specimens; **stipe** slender, usually about equalling the diameter of the disc, originating underneath the epidermis of the substratum, scarcely noticeably erumpent, smooth, usually more or less broadened at juncture with disc; **disc** at first subglobose, opening by a pore, finally expanding, more or less saucer-shaped, of medium thickness; **receptacle** smooth when fresh, very minutely radiately furrowed when dry; **hymenium** becoming plane at maturity and with maximum moisture content, drying slightly to pronouncedly concave; margin thick, obtuse; **in section:** stipe with a rind about 30 μ thick or about 5–6 cells thick, composed of longitudinally parallel hyphae 4–8 μ diam. divided into rectangular cells 13–19 μ long with walls slightly thickened and confluent, this rind enclosing a large central core of parallel, compact hyphae 2.5–3.5 μ diam. with walls slightly thickened, divided into cells 25–50 μ long; *disc* composed of an ectal layer of hyphae similar to those of the stipe and a relatively reduced medullary region of more loosely interwoven hyphae; *ectal layer* about 50 μ thick at the base, becoming thinner toward the margin, consisting of an outer zone similar to that of the stipe and a broader inner zone of radiately parallel hyphae similar to those of the central part of the stipe; paraphyses simple or frequently once or twice branched at or more often below the middle, usually near the base, 3–5-septate, slightly clavate at the apex and there 3–3.5 μ diam.; **asci** originating from croziers which break rather easily, clavate, 118–135 x 12–15 μ; **ascospores** biseriate, 1-celled, obtuse and rounded above, flattened on one side or slightly curved, narrowed downward, acute at the lower end, 24–34 x 5–6.8 μ, each end beset with 1 to several small, inconspicuous cilium-like processes, content with numerous conspicuous refractive granules.

Known from only three collections: **New York:** On old stems of *Polygonum robustius* (Small) Fernald (det. Fernald) lying in film of water in swamp, Cayuta

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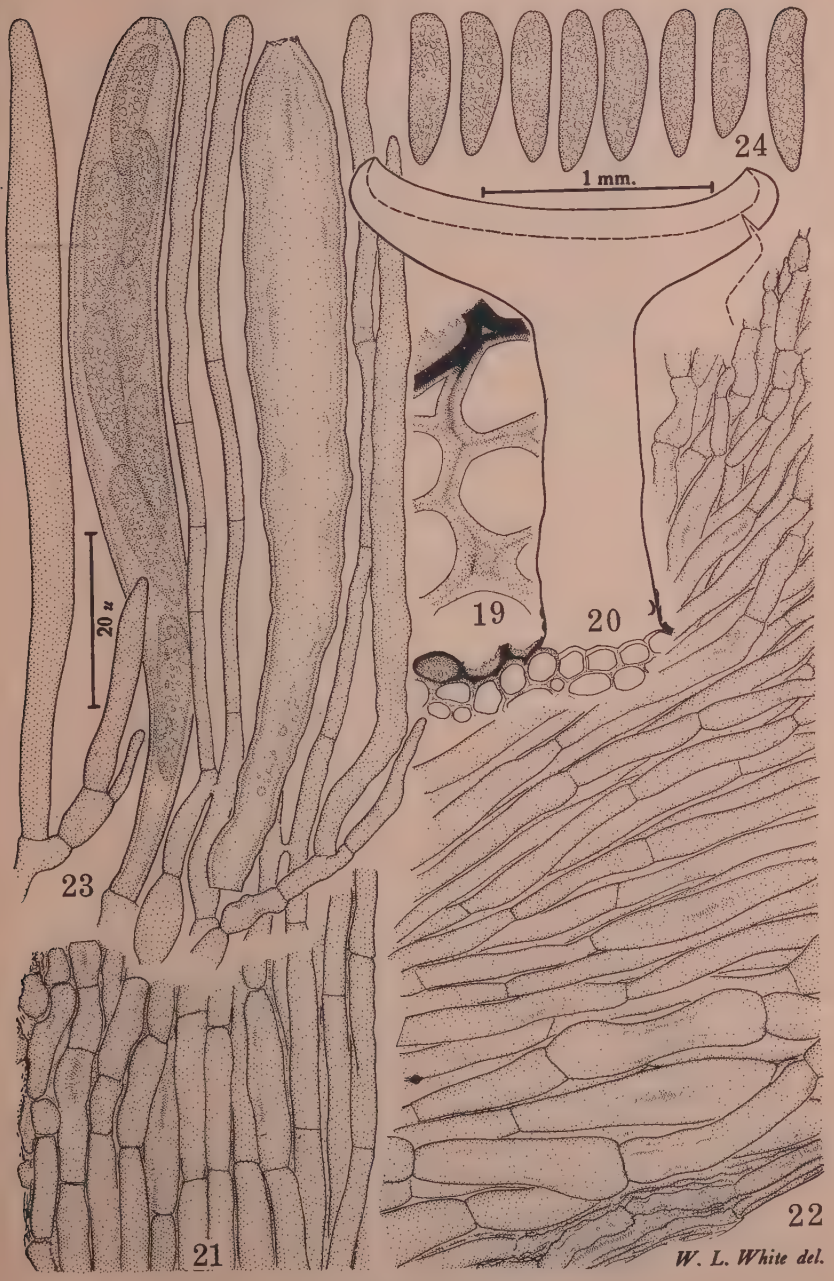
Fig. 19–24, Helotium albidum, all from **type** material, Desm. Pl. Crypt. Fr., Ed. I, *2004* (FH): **19,** Diagrammatic representation of section through an apothecium, × 40; **20,** Section showing blackening of the exposed cell walls over the area of the petiole on which the apothecia are seated, the epidermis of the petiole having earlier sloughed off, × 1290; **21,** Section showing structure of outermost tissue of stipe, exposed surface at left, taken from near but not at the base, × 1290; **22,** Section showing structure of disc tissue, × 1290; **23,** Asci and paraphyses, × 1290; **24,** Ascospores, × 1290.



FIGURES 19–24

FIGURES 25–30

Lake, Sept. 1, 1936, *H. H. Whetzel & W. L. White* (CU-P *25494*, FH, US). — Same substrate and locality, Sept. 9, 1938, *Whetzel, White, et al* (CU-P *27863*, FH, US). — **England:** "On dead stems of *Polygonum* lying in water.". Shrewsbury, Phill. Elv. Brit. *120*, **type** (CU-PD *11122*, FH).

It would be scarcely possible for three collections to agree more completely than do those cited above. Although the substratum for the British specimen is insufficient for complete identification, there is no doubt about its being *Polygonum*, and the pieces of stem in the packets agree so closely with those of the American collections that one is tempted to guess that they represent a closely allied species. The evidence is that this fungus does exist as a distinct entity within the taxonomically difficult *Helotium scutula* complex of which it is a member. Its distinguishing characteristics are the presence of croziers at the bases of the asci, relatively large asci, large and robust spores, and occurrence on decaying, water-saturated stems of *Polygonum*. Though this variety may prove to be confined to *Polygonum*, this does not mean, however, that all members of the *Helotium scutula* group found on *Polygonum* should be referred here. On the contrary several collections are at hand where the substratum is *Polygonum* and the fungi are typical *Helotium scutula*. A specimen on *Polygonum* from Iowa (CU-PD *553*), reported by Seaver under the varietal name, represents typical material of the species.

Cultures were made from both of the American collections, using mass ascospore discharge on potato dextrose agar. The spores germinated readily, becoming 1–3 septate in the process, and developing a mat of sterile mycelium. The cultures were maintained only in test tubes at room temperature, but there developed no conidial stage, spermatia, stromata or other structures of taxonomic value.

7. **Helotium Dearnessii** (Ell. & Ev.) White, Mycologia **34**: 167. 1942.

Peziza (Phialea) *Dearnessii* Ell. & Ev. nom. nud., N. Am. Fungi, second series *2624*. 1891.

Phialea Dearnessii Ell. & Ev., Proc. Acad. Nat. Sci. Philadelphia **1893**: 146. [Feb. 28] 1893. — Sacc., Syll. Fung. **11**: 403. 1895. — Seym., Host Index, p. 558, (559 from error in host det.). 1929. — J. H. Miller, Pl. Dis. Rep. Suppl. **131**: 47. Aug. 15, 1941, based on an incorrect determination.

Hymenoscypha Dearnessii (Ell. & Ev.) Kuntze, Rev. Gen. Pl. **3**^{2}: 485. 1898.

FIGURES 31–34.

Apothecia scattered to subgregarious, not crowded, appearing sessile or nearly so, in the dried condition ochraceous, all parts concolorous 0.3–0.7 mm. diam. across the disc, when moistened becoming more yel-

Fig. 25–30, Helotium scutula var. **fucata,** all except fig. 30 from Phill. Elv. Brit. *120*, **type** (FH): **25,** Diagrammatic representation of section through apothecium, × 76; **26,** Section showing structure of outermost tissue of stipe, × 1290; **27,** Section showing structure of outermost tissue of disc, × 1290; **28,** Asci and paraphyses, × 1290; **29,** Ascospores, × 1290; **30,** Ascospores germinated on potato dextrose agar, slightly more than × 1290 (CU-PD *25494*).

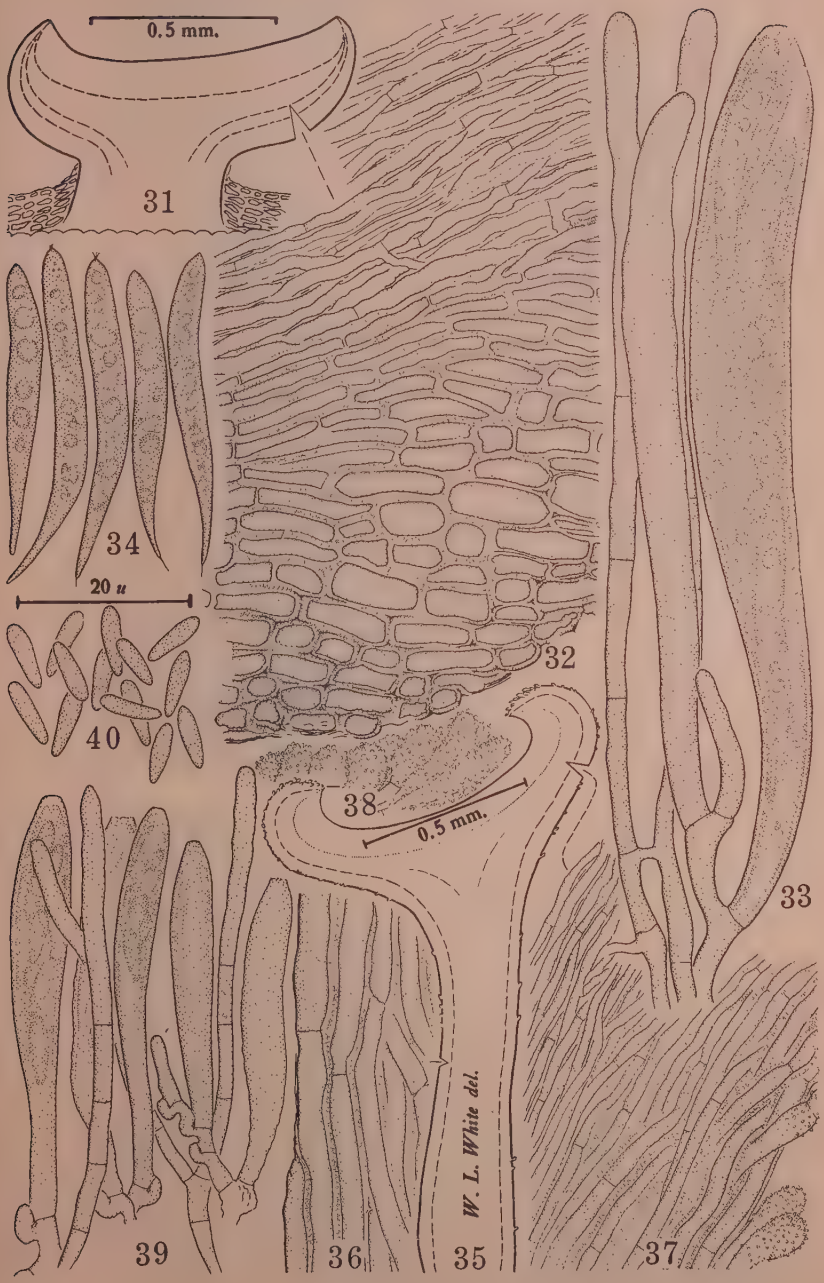
lowish the largest reaching as much as 1.0 mm.; **stipe** obscure, scarcely long enough to raise the central part of the disc off the substratum, rarely longer, ochraceous, rarely darker at the base; **disc** rather fleshy, saucer-shaped when dry, becoming cushion-shaped when moistened; **receptacle** smooth; **hymenium** opening by a minute depression, soon plane, remaining plane or becoming somewhat concave on drying, convex when moistened; **margin** even, slightly elevated when dry, when moistened expanded and recurved, wedge-shaped; **in section:** *stipe* originating underneath the cortex of the host, erumpent, cylindric, usually protruding only slightly beyond the cortex, very compact, homogeneous; *ectal layer* of disc thick, indefinite, in general composed of an inner layer originating at the top of the stipe, about 40 μ thick at the base, tapering towards the margin, colorless, composed of compact parallel hyphae about 3 μ diam. with walls scarcely or not at all thickened, these hyphae turning obliquely outward to form a thicker outer brownish zone and there becoming somewhat larger, shorter-celled, with walls thickened and confluent; *medullary region* thin, rather loose, the hyphae rather narrow, thin-walled, interwoven, becoming erect towards the hymenium; *hypothecium* not differentiated from medullary layer; **paraphyses** mostly simple, rarely once-branched below the middle, gradually enlarged from base to apex, about 3–3.5 μ diam. at apex; **asci** not originating from croziers, clavate, 100–108 x 9–13 μ; **ascospores** biseriate, elongate, pointed at the ends, attenuate below, 1-celled, containing a row of 2–9 oil globules, with a delicate cilium 2.5–3.5 μ long at the lower end, sometimes also at the upper end, 30–35 x 4–4.5 μ not including the cilia.

Known only from the following collections: **Quebec:** On old herbaceous dicotyledonous stems, Aug. 25, 1938, *J. W. Groves* (FH, OTB). — **Ontario:** On old stems of *Steironema ciliatum* (L.) Raf., London, May [24], 1890, *J. Dearness 1713*, **type** (FH-E). — Additional material from same place, June [13], 1890, *J. Dearness 1713*, Ell. & Ev. N. Am. Fungi, 2nd ser. *2624* (FH).

According to a letter from Dearness to Farlow, he first collected the species May 24, 1890 and recorded the substrate as *Monarda didyma*. Ellis described it as on *Monarda* and it was so recorded in Seymour's Host Index. Dearness apparently returned to the same place June 13, 1890, collected additional material which he sent Ellis for his N. Am. Fungi, and decided that the host was *Steironema ciliatum*. A very ample portion of the June 13th material, in addition to the portion in N. Am. Fungi, was sent to Farlow and is now in the Farlow Herbarium.

Fig. 31–34, Helotium Dearnessii, all from Dearness, *1713*, coll. June 1890 (FH); **31,** Diagrammatic representation of section through apothecium, × 64; **32,** Section showing details of structure of ectal excipulum, × 1290; **33,** Asci and paraphyses, × 1290; **34,** Ascospores, × 1290.

Fig. 35–40, Helotium gemmarum, all from CU-P *25181* (FH): **35,** Diagrammatic representation of section through an apothecium, × 60; **36,** Section showing structure of outer layer of stipe, × 1290; **37,** Section showing structure of medullary and ectal layers of disc, × 1290; **38,** Hyphal tips from margin of disc, × 1290; **39,** Asci and paraphyses, × 1290; **40,** Ascospores, × 1290.



FIGURES 31–40

The collection recorded by Miller (l. c.) from Georgia on *Steironema ciliatum*, of which he kindly loaned me a fragment, proves to be the much more common and widespread species, *Helotium scutula* (Pers. ex Fr.) Karst., to which *H. Dearnessii* is surely closely related but clearly distinct in its long, attenuate spores.

The two specimens of *Helotium Dearnessii* recorded above agree closely in their characters except that in the Ontario material the apothecia are all so short-stipitate that on superficial examination they appear sessile, whereas in the Quebec specimen most of them are distinctly stipitate; also the cilia, which are difficult to see in the former are rather distinct in the latter.

6. **Helotium gemmarum** Boud., Bull. Soc. Myc. France **4**: 81, *pl. 17, fig. 2.* 1888. — Boud., Rev. Myc. **11**: 167. 1889. — Boud., Icones Mycol. **3**: *pl. 493.* 1905–1910. — Boud., Hist. Classif. Discom. Europe, p. 112. 1907.

Phialea gemmarum (Boud.) Sacc., Syll. Fung. **8**: 271. 1889. — Oud., Enum. Syst. Fung. **2**: 61. 1920. — J. H. Miller, Pl. Dis. Rep. Suppl. **131**: 47. 1941.

FIGURES 35–40.

Apothecia scattered to subgregarious, small, delicate, slender, stipitate, white, in the fresh condition up to 1.5 mm. high (up to 5.0 mm. fide Boud.) and 0.4–1.4 mm. across the disc; **stipe** slender, slightly enlarged upward, when fresh hyaline to dilute white, smooth at the base, minutely puberulent above, not changing perceptibly on drying; **disc** opening by a pore, at first infundibuliform, at length expanding, finally plane, thin, on drying quickly contracting to become more or less funnel-shaped with margin turned inward; **receptacle** minutely and sparsely puberulent, dilute white when fresh, remaining so on drying or varying towards dingy cream-color; **hymenium** always about same color as receptacle, flat at full maturity and with maximum moisture content, otherwise more or less deeply concave; **margin** minutely puberulent, even with the hymenium in fresh, mature specimens, erect or turned inward in dried material; **paraphyses** not numerous, simple or more rarely once-branched below the middle, not enlarged at the apex; **asci** small, cylindric, clavate, 45–50 x 5–7 μ; **ascospores** small, obpiriform, 6–9 x 2.5–3 μ.

Habitat: Appearing in early spring on the scales of buds of various species of *Populus* (listed below) which had fallen the previous season and lodged under and among debris on wet ground.

Distribution and specimens examined: **New York**: On *P. candicans* Ait., Lloyd Preserve, McLean, Apr. 26, 1936, *H. H. Whetzel, D. H. Linder, & W. L. White* (CU-P *25181*, FH). — On *P. candicans*, Lloyd Preserve, McLean, May 2, 1937, *W. L. White et al* (FH). — On *P. candicans*, Lloyd Preserve, McLean, May 18, 1940, *H. H. Whetzel, W. L. White, & J. Niederhauser* (CU-P *29086*, FH). — **Pennsylvania**: On *Populus* sp. ?, May 5, 1935, *H. H. Whetzel* (FH). — **Georgia**: On *P. deltoides* Marsh., Agricultural Campus, Athens, Apr. 29, 1940, *J. H. Miller* (GA *583*). — **France**: Type locality. Boudier indicated that it was frequent on the old bud scales of *Populus nigra* L. in the vicinity of Paris in February. Notes and drawings by Massee, made from Boudier material, are in the New York Botanical Garden but are not accompanied by a specimen.

There appears to be no European material of this species available in the herbaria of this country. However, it is well marked as to morphological characters, substratum, and season of occurrence. Comparison of North American specimens with the illustrations of Boudier leaves no reason for doubt as to its identity. Two other species with similar characteristics — white, slender, with small spores, occurring in the spring in moist habitats — and possibly more or less closely related, are *Phialea Cassandrae* Kanouse, occurring in Michigan on the leaves of *Chamaedaphne calyculata* (L.) Moench (see White, Farlowia **1**: 159. 1943), and *Helotium amenti* (Batsch ex Fr.) Fuckel (see Boudier, Icon. Mycol., pl. *496*. 1905–10), of widespread occurrence on female catkins of *Salix* sp.

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REVIEWS

UEBER DIE BEDINGUNGEN DER MYKORRHIZABILDUNG BEI KIEFER UND FICHTE. By Erik Björkman. Uppsala. Symbolae Botanicae Upsaliensis. Vol. VI, no. 2. 1942.

When B. Frank (1885) likened the common fungus root of a tree to a factory operating for its own profit, he was not unmindful that the tangled and swollen root tips of a tree with their covering mantle of fungous skin, and their cakes of mycelia between the cells, look like witches brooms or other gall formations caused by a parasitic fungus. He considered that the fungus obtained its food from the host tree and in return provided the tree with water and nutrients for growth, which the fungus extracted from the soil through its widespread mycelial threads. This interpretation did justice to what one can see, and it is supported by much else: many nutrients are deficient in the raw forest humus (mår) (Stahl 1900); the fungus root is built like an organ for the exchange of substances (Mangin 1910); Neger (1913) found more sugar in roots from trees which habitually have fungus roots than in the case of ash and many other plants; Rexhausen (1920) found plenty of fungous starch (glycogen) in the mycelium of root fungi and more sugar or starch in infected roots than in other roots of the same tree; a number of large fungi of the forest known to form mycorrhiza (Melin 1922–25 et al) follow their host trees as a "dolphin follows a ship." Lange (1923), also Thesleff (1919), Romell (1921) and Melin (1925) did not admit that the mycorrhizal agency can consume cellulose or the more common energy-giving foods, except sugar; mycorrhizae can be abundant in almost completely humus-free soil, such as volcanic ash (McDougall and Jacob 1927); soluble dyestuffs can penetrate the fungus membrane and mycorrhizal net right into the cells of the host tree (Endrigkeit 1937); conifer seedlings without or almost without mycorrhizae have shown a lower phosphorus content and most of them also a lower nitrogen and calcium content than plants with abundant mycorrhizae grown in the same soil (Hatch et al 1937).

Frank soon abandoned his first explanation of fungus-infected tree roots. Led astray by the peculiar pine vegetation and by some experiments with tree seedlings which he could not explain correctly, he concluded that the fungus gets no nourishment from the root, but like other soil fungi lives on humus, and only lives in the mycorrhizal covering in return for an ample rental, especially of nitrogenous substances. This interpretation was adopted more or less faithfully by most of those who wished to believe that mycorrhizae are useful to the tree. Fungi came to appear as inseparable thralls of the host plant, and one cared little about what pleasure they could get from being tenants in the roots. Nor did Stahl care either, although his explanation of fungus-infected roots of vegetables, after another manner, came near to the old theory of Frank. Quite generally one has hesitated to believe that fungi that do not penetrate into the root cells and there become digested, can do the tree any other service than common soil fungi do by forming useful substances or consuming harmful ones. Some have wished to attribute the benefits of root fungi to this (Tubeuf 1896, Rayner 1934, Burges 1936, and Lindquist 1939) but it leaves the formation of mycorrhizae unexplained, as Endrigkeit (1937) and Hatch (1937) have pointed out. Others have not been able to escape the thought that the tree's mycorrhizal builders live on their hosts. It used to awaken doubt that the mycorrhiza can be of any use to the tree, since biologists have become increasingly unwilling to conceive of any peaceful exchange to mutual advantage outside the realm of human beings. Frank's Danish pupil Sarauw (1893) and Stahl's pupil Weyland (1912) could believe no more than R. Hartig, Ramann McDougall (up to 1927) and others, that the mycorrhizal partner of trees is anything more than a harmless sponger.

Melin tried in 1925 to unite the current opinions by sifting out differences between other kinds of mycorrhizae and the common tree mycorrhizae. He had to class fungi as parasites or saprophytes, but showed that they invade root cells more frequently

than generally appears, and there they are consumed. Thereby the trees, in exchange for growth substances and carbohydrates, receive nitrogenous foods rich in carbon which the fungi have formed from substances in the raw humus that are resistant to decomposition. Thus neither of the partners needs to get the short end of the bargain, even if one calculates the calories exchanged. The theory failed of proof, for, with culture in mår, conifer seedlings with their mycorrhizae showed that they required ordinary nitrogenous nutrients; they could therefore not live on the nitrogenous staples of the mår (Hesselman and Melin 1927). In addition, Hatch (1937) found that seedlings get along just as well without fungi, with both the "more complicated" nitrogenous compounds (peptone and nucleic acid) which Melin had utilized in the experiment on which he had based his conclusions.

Hatch in 1937 forgot what Melin's experiment with different carbon sources had shown, and suggested that the mycorrhiza-forming fungi were consumed with small amounts of growth substances, "and perhaps sometimes carbohydrates". Endrigkeit the same year expressed the opinion that the mycelial net in the fully-developed mycorrhiza cannot obtain any nourishment from the host plant. The reviewer, on the other hand (Romell 1939) held that there was an exchange of substances according to Frank's first belief, and supported this hypothesis with new reasons: a fungus does active duty in place of roots and root hairs and does not need to draw on the plant more than the ordinary root system would do.

In order to be able to extract nutrients for growth from the soil as efficiently as possible in competition with all other fungi, the mycorrhizal fungi ought to have some kind of monopoly on easily digested energy-yielding food. Otherwise there seems to be no one since Rexhausen (1920) who has given Frank's 1885 hypothesis any clear support.

But here comes a young Swedish investigator and rejuvenates in new and improved form the very oldest theory for tree mycorrhiza as a useful structure. He does this by solving a riddle which has baffled investigators the world over during a generation. The mystery for which Björkman has sought the solution is the peculiar variation in abundance of mycorrhizae. They are commonly found abundantly in moderately good and better mår humus, but sparingly in the most infertile mår and often also in mull, where they sometimes are absent.

Recently only Hatch (1937) seems to have interpreted the fact, as far as it now goes, after the classical manner, namely that mycorrhizae are formed when the trees need them because they do not have enough mineral nutrients. This is no factual proof; Melin (1922–27) tried to obtain one and suggested that root fungi did not thrive in pronounced, but only in slightly acid mull (an unsupported supposition) and had insufficient "virulence" in bad mår. The word virulence is borrowed from medical science, literally meaning poisonousness, and connotes capacity to attack. But this power to attack is supposed to be explained by the word virulence. Of such a contorted phraseology Heribert-Nilsson says: "Such an explanation is as scant an aid as if a physician should stand up and declare that the cause of infantile paralysis lies in the susceptibility of man for infantile paralysis." The word virulence is yet not altogether empty of meaning. Back of it lies the thought that the tree root and fungus are in a feud with each other. But the thought carried at once difficulties. Melin (1922) first supposed, as was natural, and as later McDougall did, that the fungus must be more virulent in order to penetrate the cells than to grow between them. The next year he had to contradict this and suppose something as strange as that a less virulent fungus goes between the cells, but a more virulent one can be forced by the host plant to hold itself in the cell walls. Melin's speculative fabric has nevertheless appeared to be the best to be had, and M. C. Rayner has gratefully elaborated it further.

Björkman sought first a foundation by collecting statistics on the abundance of mycorrhizae in different forest types. This yielded him as little as his less diligent predecessors had found, as far as providing a key or even any clue, and the fifty pages which deal with this serve best some academic requirement. Inoculated pure

cultures repaid his efforts better, but still the work would have had almost the same value without them. The scientific importance of the study lies partly in the ecologically planned experiments where uninoculated pine or spruce seedlings were grown in the same soil (rich mull, better and poorer mur and peat) with their natural content of soil life, or at least of sources of life, and partly in the theory to which the experiments led. It shows that Björkman's discovery is not a result of modern technique and the work of mycorrhiza investigators of recent times, but could have been made fifty years ago if someone then had been equally industrious and had had the vital spark.

Six soils were tested in the experiment, some without additions, others under different degrees of illumination up to four soils with different additions of nutrients, and three soils under varying light and additions of nitrogen and phosphorus fertilizers. Mycorrhizae were formed abundantly even in rich beech forest mull, after a moderate mixture of sawdust which decreased the nitrogenous food content. It is, therefore, not as Melin believed, that no mycorrhizae thrive in well-developed mull. Mycorrhizae are formed abundantly also in the soils showing the highest nitrogen content (far higher than are found in nature in the richest mull) if only phosphorus is low and light is strong enough. Lindquist (1932) also was mistaken when he thought that nitrate formation is to be looked upon as a "change in dominance" in the fungous flora of the soil of such a kind that mycorrhizal formation is thereby retarded.

During the entire course of the experiments, three things were decisive: light, and the nitrogen and phosphorus contents of the soil. Thus mycorrhizae were formed in weak light (1/16 or sometimes 1/8 of full sunlight). With increased light there were steadily better seedlings with more mycorrhizae. On the contrary there were most mycorrhizae (but not the best seedlings) with moderate deficiency of nitrogen and phosphorus or both. Greater deficiency of nitrogen resulted in weak seedlings with few or no mycorrhizae. The same results were obtained in inoculated pure cultures when there was great deficiency of phosphorus. In soils richly fertilized with nitrogen and phosphorus the plants grew strongest, but had no mycorrhizae. The interaction between light and contents of nitrogen and phosphorus led to intricate correlations which are shown clearly in the report by means of three-dimensional curves.

The action of light was known before, as a result of another study by Björkman (1940) together with Hesselman. The per cent of mycorrhizae in connection with light gives curves which appear logarithmic and call to mind Stålfelt's photosynthesis curves for pine and spruce. Björkman guessed even in 1940 that there might be a connection between assimilation and mycorrhizal formation. This Melin (1927) had rejected as a possible cause for the stronger plants in Hesselman's experiment having more abundant mycorrhizae; but he did not find the interpretation worth discussing seriously.

Out of the guesses of 1940 eventually resulted the following: the mycorrhizae seek soluble carbohydrates in the root, and they consume them for energy, but they find them only if there is a surplus of carbohydrate in the root. Whether or not there is any surplus depends on the head-start photosynthesis (carbohydrate formation) has attained in the plant before the formation of albuminous substances. This advantage will be small or nil if there is an abundance of all plant foods including nitrogen and phosphorus, so that there will not need to be a shortage of materials when albuminous substances are built up. Then there will be little for the fungi to seek after in the root, and mycorrhizae will be formed sparingly or not at all. On the other hand, should there be a deficiency of nitrogen or phosphorus foods, there can easily arise a surplus of carbohydrates so that the formation of albuminous substances falls behind photosynthesis. With a moderate lack of nitrogen or phosphorus or both, mycorrhizae can form abundantly, but if there is a serious lack of nitrogen or phosphorus, sooner or later photosynthesis will become weak also (phosphorus especially strongly influences carbohydrate formation in plants) so that the surplus of assimilated carbohydrate becomes less for that reason, and mycorrhizae are formed more rarely. Similar reactions occur if light becomes weak. *Mycorrhizal formation*

is, expressed briefly, a result of and a sign that there is a certain surplus of energy-giving nourishment in the host plant.

Björkman's theory is this simple, but it is confirmed not only by his own involved curves, but also by what is otherwise known. A direct support for it is the higher sugar content that Rexhausen found in mycorrhizal roots. Björkman himself has found a still clearer direct support for his theory. In two experimental series he determined the amount of "reducing substance" in the roots of seedlings (in plain language — simple kinds of sugar; also many other substances according to Björkman). He who takes time to plot the data against the percentages of mycorrhizae (which Björkman should have done himself) finds a beautiful correlation. It is especially noteworthy that the relationship is so similar in two different soils.

However, not even such a prop for a theory is any final proof of it, and questions remain. How does the fungus know that there is surplus sugar in the root? Does it go and feel here and there, or does the root give off sugar or something else tempting when assimilation begins to satiate it? Still there does not seem to be room for any major error in Björkman's theory.

It is clear, although Björkman has not wished to say so, that Melin's virulence theory has a reversed picture of reality. Whether mycorrhizae are formed or not depends more on the host plant than on the fungus, rather than as Melin and others have believed. The old scoffing belief that mycorrhizae are formed when the plant needs them came much nearer the truth, for a surplus of energy-giving food, which actually is the deciding factor, is conditioned in turn by a deficiency of mineral nutrients (C/N ratio). Among recent investigators Hatch came nearest the truth (as Björkman mentions rather cursorily) by his hypothesis that mycorrhizae are formed when there is too low a content in the plant of one or another of a number of nutrient substances.

Björkman's work throws new light not only on the problem with which he has been especially occupied. The solution he found to this question falls at once as a judgment of Solomon on the old strife between the "nitrogen theory" and "salt theory" of the ecology of mycorrhiza. It shows both theories to be more or less correct, but erects in their places a new, simple and beautiful theory, with an inner strength which no other mycorrhizal theory has had, for it gives an actual well-grounded explanation which appears axiomatic when it has once been clearly apprehended.

The new theory should be called the Frank-Björkman, for it is a deepened and expanded form of Frank's old one. According to it the mycorrhiza comes more than ever to appear like a factory for mutual profit. False must be called the whole viewpoint now for some time considered the only scientific one the world round: that altogether too human fable of the brutal burglar or the company formed by two gangsters who steal from each other. The exchange of substances in the mycorrhiza appears instead as a peaceful exchange where one party gains from the other's unnecessary surplus, by offering goods he lacks in his activity, or if one will, by hiring and paying an industrious servant. Probably never before has anyone shown so clearly how the ways of nature can lead to a symbiosis between plants to their mutual advantage, and how this living together in many cases must inevitably take on this form just because an exchange serves its needs. Björkman's work is destined to make a deep imprint on biological thinking in due time. His theory may furnish the key to the mystery of the symbiosis of alder and its nodule former, and perhaps also that of legumes and their root bacteria.

A theory of such breadth as Björkman's raises the question of exactly how it came about. One can read that it grew out of the hypothesis that the organisms forming mycorrhizae live on their host trees, and from Björkman's interpretation of 1940 based upon it, of the effect of light upon mycorrhizal formation. However it is far from there to the complete theory. One thing and another suggest that Björkman almost brought out his work without its real point. Probably he came upon the solution when he read in the literature about the influence of phosphorus on the sugar con-

tent of beets and other plants, and about nodule formation on roots of legumes where the carbon-nitrogen ratio is at present considered to be the controlling factor. In such cases it is proof that there can be a certain value to the learning they are wont to have in Swedish doctorate dissertations. It in no wise follows from the above, however, that Björkman got his theory without effort, or even that almost anyone could have hit upon the solution by reading the literature. Others before this have brushed lightly past the key Björkman found, but have not seen it.

If spruce seedlings die out on mull rich in nitrate, then it cannot reasonably be attributed to their failure to get the mycorrhizae they need (Lindquist 1932). When they do not have mycorrhizae it is on the contrary a proof that they do not lack any nutrient that is consumed in further elaboration of the first formed carbohydrates, and it is probably because they lack light.

Black mycorrhizae are no sign that the soil is sick or cold so that a cutting must be made (Lindquist 1937). It indicates only weak light, that is, the stand is unusually dense for northern Sweden. It must always remain a difficult task to judge the soil by the mycorrhizae, since poor mycorrhizal formation can depend either upon high nitrogen and phosphorus nutrition, or too little of either or both, or too scant light. Now perhaps it can be done in certain cases, thanks to what we know through Björkman. — Lars-Gunnar Romell in *Svenska Skogsvårdsföreningens Tidskrift. Häft IV. 1942.* [Translated by H. I. Baldwin]

RECHERCHES SUR LES CÉRAMIACÉES DE LA MÉDITERRANÉE OCCIDENTALE. By G. Feldmann-Mazoyer. Algiers, Imprimerie Minerva, 1940 (1941). 510 pp. 191 text figs. 4 pls.

In this important memoir, Mme. Feldmann-Mazoyer has presented the results of many years of research prosecuted in the Laboratory of Botany of the Faculty of Sciences of Algiers and in the marine biological stations of the Faculty of Sciences of Paris at Banyuls and Villefranche.

The researches of the author deal with: 1) the cytology of the Ceramiaceae, 2) the morphology of their vegetative structures, 3) their reproduction, and 4) their taxonomy. In these four series of researches, the author has obtained new results and has clarified questions which until now have remained obscure.

In the parts devoted to cytology, the membrane, the nucleus, the cytoplasm and its elements, and the products elaborated by the cell (special floridean starch, osmophilic granulations, basophilic bodies, . . .) are studied successively. The author makes many new contributions to the knowledge of the floridean cell, notably as it concerns the structure of the membrane, the morphology and the variations of the plastids, the structure and metabolism of floridean starch, etc. She has particularly studied the secretory cells, "bromuques," which according to Sauvageau contain free bromine. By new microchemical methods she has been able to establish the absence of free bromine in these cells. Also, the study of intercellular relations has permitted her to uncover in the axial cells, structures which are active in the translocation of dissolved nutrient substances, the structures playing the rôle that had been attributed to the cells themselves. She has been able to confirm experimentally the rôle attributed to the synapses in these phenomena.

In the portion devoted to the morphology of the vegetative structures, the author has been able to clarify structures heretofore poorly known. She has shown in particular that the verticillate epidermis of species of *Griffithsia* correspond to the trichoblasts of the Rhodomelaceae and has demonstrated their function as an absorptive layer.

In the part treating with reproduction, the author has been able to describe the development of the reproductive organs in certain genera and species in which this was poorly known or even completely unknown.

The systematic part constitutes a veritable monograph of the Ceramiaceae of the western Mediterranean. Using the results of researches enumerated above, the author

has ben able to establish a more rational classification of the family based principally on the structure of the procarp, in part on the manner of development of the gonimoblast, and in part on the cytological structure. She has established three new tribes and modified the limits of many others, has created three new genera and suppressed four. She has described some new species and on the contrary has suppressed a large number, the study of very abundant living material having permitted her to determine that these so-called species represented only seasonal or ecologic variations.

In each genus, very carefully prepared dichotomous keys permit the determination of the species which are later described in detail. Numerous illustrations facilitate further and render more certain this determination.

The work of Mme. Feldmann will remain the basis of all studies of the Ceramiaceae, not only in the western Mediterranean, but of the entire world. Its great merit is that it was founded not only on herbarium material, but more especially on living plants, and that it has correlated, thanks to this fact, the numerous physiological and cytological characters with the purely morphological concepts of the earlier algologists.

—R. Maire [Translated by D.H.L.]

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